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THE « AGARICALES » (MUSHROOMS) IN MODERN TAXONOMY

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Dedicated to the memory of Victor Fayod and Narcisse Patouillard.

GENERAL INTRODUCTION

Progress in the knowledge of the taxonomy of the *Basidiomycetes* as a whole is most evident in the *Agaricales*, a group that can be roughly characterized as consisting of « agarics » and « boletes », or, in common language « mushrooms » and « toadstools ». It may, however, be stressing a point if such minute fungi as *Flagelloscypha minutissima* — never noticed by those hunting the woods for mushrooms, and hardly recognized as mushrooms by the amateur — are put in the same category as such giants as *Phlebopus colossus* or *Leucopaxillus giganteus*. Yet they belong in the same order according to our present views on systematics, which are based on what we recognize as affinity rather than on any one specific character. Consequently, the definition of the order *Agaricales* has changed in recent years to become too complicated to be expressed in a customary short diagnosis (see however p. 129). The non-taxonomist may justly ask: Is this complication really worth while?

We taxonomists think our results are fully worth the trouble of reshifting the classification, worth the application of more and more time-absorbing methods of investigation, worth the inconvenience of the necessary changes in generic and specific names, and worth the opposition of some of our colleagues working in other fields who may denounce our inability to state shortly and simply the characters on

which the groups of fungi are separated. We think so because an approximately natural classification does not only make mycological work more precise but more applicable in neighboring fields. It makes it easier to substantiate or refute theories of evolution, or at least more nearly to achieve one of the two main objectives of systematic biology — the one usually neglected — namely the assembling of related groups and forms in taxonomic units. Accurate identification is certainly needed by physiologists, plant pathologists, medical mycologists, foresters, biochemists, plant geographers, ecologists, and mycophagists but it cannot be obtained by simplified methods. If two identical fungi are currently erroneously determined as different species, or vice versa, results of all investigations using these organisms as testing material become doubtful unless herbarium material with notes and correct data are preserved, a precaution practically never taken, or if taken, rarely used for comparative studies on the material pertaining to contradictory statements. The biologist who is not a taxonomist will either try to make his determinations by a simplified method, or call on a taxonomist for cooperation. In either case — thanks to the lack of good books for identification, and the lack of a sufficient number of able taxonomists in the *Agaricales* as well as in many other groups of the fungi — the results are not too good. Nevertheless, a good taxonomist is now able to identify a species of *Agaricales* with much more accuracy than fifty years ago. The introduction of new characters always leads to clearer delimitations between genera and more accurate distinctions between species so that more precise determinations can be made because the number of characters that must fit into a diagnosis is larger, and the characters themselves are more definitive. Consequently, the sharpness of our modern species concepts by far surpasses that of those found in the older taxonomic works. Who does not remember such characters as the incurved margin of the *Collybiae* and the straight margin of the *Mycenae* projected into groups such as *Rhodophyllus* and *Psathyrella* where they have no meaning and in which they made identification a guessing game rather than scientific work.

Advance in some related fields often depends on the right choice of material, i. e. the proper organism to start the experiment. The basidiomycetes tested previously for antibiotic substances have been shown to contain such compounds in many species and « strains » in one taxonomic group, and none in another. It is quite obvious that the question whether such a group is a natural unit or an artificial

one has some importance on practical planning for further testing. If for instance it is planned to take a number of promising organisms in culture and test them quantitatively for bacteriostatic substances after preliminary tests on various groups of representative species have already shown in which genera species of this kind occur, time and effort can be saved if the work is organized on the basis of a working hypothesis assuming that the genera known to contain some bacteriostatic forms are richer in these than are the genera where no such forms have thus far been discovered. In fact, this is approximately the way in which research is usually planned. If *Stropharia* were still combined with *Agaricus* in a single tribus *Psaliota* as it was, against all natural affinity in Fries' early classifications, it is to be expected that the promising group of *Agaricus* and the thus far not too promising group of the *Strophariae* would have been studied together in any work planned on antibiotics, thus — because of the lack of a natural classification — causing unnecessary expansion of the testing program, and more time and expenditure would have been necessary. In the *Boletaceae*, only the genus *Boletus*, as far as known, contains antibiotic substances; in the *Tricholomataceae* — *Tricholomopsis* and *Lepista* seem to be most important in this regard; all these genera are rather recently established units, and in the older units (*Boletus* sensu lato, *Tricholoma*, *Clitocybe*, etc.) the results of the testing as published by Wilkins and Harris appear to be uncorrelated and without any recognizable connection with taxonomic units. This and similar examples taken from the chemical and physiological literature show clearly enough that the more artificial a classification, the longer the pertinent facts will remain hidden; the faster the progress in taxonomy, the more guidance will be available for investigators in neighboring fields engaged in studies on organisms belonging to this particular taxonomic group. In the older classification, the specificity of the mycorrhizal relation was an unpredictable, coincidental character of the species of the *Boletaceae*. Now we know that the mycorrhiza-relationship is closely connected with the taxonomic position of a species, and the forester can be sure whenever encountering a species of the subfamily *Suilloideae* that this organism is forming mycorrhiza with certain conifers of a stand of trees, even if the forest is a mixed one. Going one step farther — when the section of the genus is known, the bolete can easily be linked with a definite genus of conifers in most cases, and many of the species are selective enough to be found, in nature, only with one species of

higher plants, or even with one race only. Here again, a hypothesis on the basis of field observations generalizing the results obtained in experimental studies on a few species of a genus will result in a wiser and more intelligent selection of the organisms when a research plan on mycorrhiza is made. Correct identification and a valid concept of affinities is also essential in the new field of ecology-geobotany.

The taxonomists being few, and the problems being so many, it appears that there is much less justification for questioning the usefulness of the modern development of the taxonomy of the *Agaricales* and the fungi generally than there is for an answer to the question why so few able persons are attracted by this important field of natural science. In fact, taxonomy of the fungi, more than other branches of the sciences, suffers from understaffing and lack of support. This is felt even more severely since taxonomy of many cryptogamic groups has completely grown out of the reach of the type of amateur whose contributions, not so long ago, played a major part in the development of the taxonomy of the *Agaricales*. Since an accurate, methodical determination of a species of *Agaricales* now requires very high botanical and technical skill, the average mycophagist can no longer follow the development of taxonomy.

On the other hand, the talented and interested student of biology has, as a rule, little reason to become enthusiastic about systematics, at least as taught at present in the field of *Agaricales*. The matter seemed to be — and actually was, with a few notable exceptions — on a desperately non-scientific footing, and as far as college instruction goes, it persists to be essentially an assemblage of unrelated and unexplained facts, with numerous terms and scientific names (used in a different way by each author), and a few perennial myths thrown in. The anatomical features of the *Agaricales* have been neglected, and the rôle of these fungi in applied biology is represented as practically confined to wood-destroying properties and edible qualities of some of the species.

With new problems of general interest developing in the mycological field, especially the *Agaricales*, e. g. production of new antibiotics, control and application of symbiosis in forestry and horticulture, control and eradication of tropical crop diseases in plant pathology, and, to some extent, prevention of fungus-caused deterioration of fabrics, especially in the tropics, it is a matter of serious concern whether or not enough specialists can be interested in the study of the *Agaricales*, particularly in a study of their taxonomy, to cope with these new problems.

The difficulty consists mainly in the fact that the non specialist is unable to find his way in the widely scattered papers that contain fragmentary information on modern concepts of taxonomy in the *Agaricales.* Even if he knew which papers to choose, he would still have to face the tremendous task of coordinating the data obtained, and presenting them to others in a scholarly way. There has also been too much needless splitting of genera and species in the past, so much renaming and ruthless synonymizing [1] that, as a consequence, a certain hesitancy in accepting new combinations, new generic names, and new status has developed — a conservative attitude among non-specialists that is quite understandable. This must lead to a situation equally bewildering to the teacher and the student wherever the names applied in contemporary manuals and text books are at variance. This is also hindering the work of the curators in herbaria, the authors of local floras, the ecologist (especially the geobotanist), and generally anybody interested in Higher *Basidiomycetes.*

Under these circumstances the author felt that a comprehensive presentation of modern taxonomy is a definite need. The task is a large and difficult one merely from the standpoint of the time that the preparation of a book of this kind takes when compared with the pace at which taxonomy progresses. There will be those who feel that the book is not complete enough, and there will be others who disagree on certain details claiming that they do not fit into a true picture of modern taxonomy. The policy in writing this book was to indicate as facts only those data that were established as facts on authentic or otherwise reliable material by the author himself, or by other authors that the writer considered as absolutely trustworthy in a given case. The latter course, however, was seldom taken, and it may be said that the vast majority of data contained in this book are based on the author's own investigations, including the insertion of every single species at its proper place in the classification. Consequently, additional data would have required additional type studies, but it seemed desirable to set a time limit if the book was to appear in the near future. There are, of course, minor differences of opinion among the taxonomists, especially as to the conception of the genus, which the author believes is now approximately compara-

[1] The fact that we must now take up some of the names then proposed, because the rules of nomenclature force us to do so, does not justify them posthumously.

ble with the prevalent conception of the generic unit in the *Cormophyta.*

The book cannot and will not be a monograph. Complete synonymy is given only for the genera. The synonyms of the species which are indicated as examples rather than as a complete enumeration, are given in brackets and concern only the binomials most frequently found in the literature as well as those necessary for the understanding of the transfer if such a change has been made recently. The most conspicuous inconsistency will be noticed in the keys to the species. Such keys are given only if they do not duplicate good keys in easily available monographs or floras (which are cited), and if it is possible in a given genus, according to our present knowledge, to write a useful key. On the other hand, the insertion of the keys available was considered necessary because of the legitimate desire of the reader to know just how to go about the identification of the species in each genus.

The paragraphs on the limits of each genus and on the state of knowledge concerning it were introduced in order to show exactly what difficulties, if such exist, one is still likely to encounter in a given group, and along which lines an improvement is thought to be possible. This procedure will, in the author's opinion, help further monographic studies, and at the same time avoid the impression of an accomplished knowledge of all aspects of a problem — an impression so often conveyed in text books.

The modern taxonomists have a right to present with confidence a summary of their work as the interim results of various and numerous studies on an enormous amount of material. It is, however, a duty of justice and gratitude to acknowledge the invaluable work done by the great forerunners of our era. They have pioneered in the exploration of the anatomy of the *Agaricales,* and their contributions toward a natural system of classification are amazing to those who look back in the historial perspective. Only the genius inspiration of these men explains many of their discoveries in the taxonomic field — such as the recognition of the affinity between *Dictyopanus* and *Panellus* by Patouillard — that can be fully appreciated only now. These are the reasons why this book is dedicated to the memory of Victor Fayod and Narcisse Patouillard (Plate I, 2).

It is a pleasure to express the author's gratitude to the many curators of priceless collections who have furthered this work by generous loans of type material from all over the world, and also to

my friends who have discussed frankly and amically many problems in personal meeting and in correspondence, especially Dr. M. A. Donk, Buitenzorg; Dr. R. Heim, Paris; Dr. D. H. Linder (†); Dr. Henri Romagnesi, Paris; Dr. Alexander H. Smith, Ann Arbor; Dr. W. H. Snell, Providence; Dr. W. H. Tranzschel (†).

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CRITICAL SURVEY OF THE CHARACTERS OF THE *AGARICALES* AS THE BASIS OF THEIR TAXONOMY

The basic characters used by taxonomists in the field of Higher *Basidiomycetes* have twice been augmented and revised in the history of systematics. We shall not review the characters on which the Persoonian and Friesian systems of classification were based, nor shall we repeat the fundamental discoveries in the field of anatomy and the revaluation of certain macroscopical characters that have taken place in the second half of the past century, inspired by the general search for the « Natural Classification » of the fungi, and by the activities of such influential mycologists as de Bary. All these facts are now duly understood and can be found in any good text book on mycology. The present treatment starts where a new development has taken the lead without as yet offering a comprehensive resumé of facts and results. The author (1936) has discussed this last period (starting in the early twenties of this century) as the third period in the development of systematics in the *Agaricales*, characterized by an immense accumulation or additional descriptive facts and new theories to explain them. The resulting modification in the appraisal of certain known characters and the addition of new characters now considered important is the subject of the following chapters.

I. THE VEIL

The veil in the widest sense, i. e. the involucrum in Persoon's terminology has been considered as being of the utmost importance in taxonomy as far as Fries and his school were concerned, and an improportionate overemphasis was put on it in such classifications

as those proposed by Karsten, Schröter, and especially Earle. This was partly understandable since the veil was considered as a first step toward the higher forms, or rather a criterion of higher forms as such. It is only fair to mention here that some authors still continue to think so — however with certain modifications, based on the difference in interpretation of veils.

Several basically different organs have been confused in the term « veil »

1. *The volva.* This is a general enveloping layer in the « egg stage » of the carpophores and subjects the primordium to a certain centripetal pressure. It is never thin and arachnoid. A volva has been observed in the *Agaricaceae* (*Clarkeinda*), the *Amanitaceae* (*Termitomyces*, *Amanita*, *Volvariella*), the *Coprinaceae* (*Coprinus* spp., *Macrometrula*), and in a more reduced, indistinct or fugacious form in other related genera. In all these forms, the volva remains more or less distinct in the adult carpophores as a cup or concentric scales at the base of the stipe, and/or as coarse warts or volva-patches on the surface of the pileus. Parts of double annuli viz. the outer-lower portion of the annulus of *Catathelasma* and some species of *Agaricus*, probably also *Rozites*, may logically be considered as a special form of volva where, on the lower part of the stipe, the volva is appressed or reduced to an innate covering. (Atkinson's blematogene). The annuliform, i. e. ring-like portion of the volva may be referred to as an « annular volva » or the «volval portion of the annulus ». The counterpart of the agaric volva in the *Gastromycetes* is the volva or so-called peridium of the *Phallineae,* the genera *Montagnea*, *Gyrophragmium*, *Battaraea*, some species of *Tulostoma*, and *Torrendia.*

2. *The pellicular veil and the cortina.* These are remnants of a layer or all the layers of the cortical tissue of the primordium, and are later ruptured by the expansion of the pileus whereby they are extended and thinned. If the cortical layer is gelatinized and the stipe absent, this kind of veil is called pellicular veil by Lohwag; if it is dry and arachnoid, and the carpophores are stipitate, it is, since Friesian times, called cortina. Both pellicular veil and cortina are essentially the products of hemiangiocarpous development of the hymenophore in the young carpophores, and should not be applied unless it is reasonably certain that the organ referred to belongs to a species with hemiangiocarpous development. The thinness of this veil is an important feature because the layer taking part in its formation is a thin layer from the start, and is reduced by the tension

from the margin when the pileus expands. It is conceivable that, phylogenetically, the pellicular veil as well as the cortina may be derived from the volva.

3 *The marginal veil.* This type of veil formation is due to the incurving margin whereby the covering layer of the apex of the stipe is brought in intimate contact with the tissue of the margin of the pileus. Later, when the pileus is expanded, the separation may not take place exactly at the plane of the original contact but parts of the marginal tissue take part in the formation of an organ that consists largely of an outgrowth of both marginal and stipe-hyphae, and is stretched by the reopening or the margin. If the final separation takes place near the surface of the stipe, the marginal veil will then hang down from, or adhere to the margin of the pileus; if, however, the separation takes place farther outside, an annulus will be formed that remains on the apex of the stipe or slides down it. In the first case, it is called velar appendiculation of the margin, in the second, marginal annulus on the stipe. If separation takes place on both stipe and margin of the pileus, the annulus mobilis results. The marginal veil can best be studied on such species as *Boletinus cavipes* or *B. appendiculatus*, in *Macrolepiota procera*, *Chlorophyllum molybdites*, etc. In the two species of *Boletinus* the development of the hymenophore in the young carpophores is pseudoangiocarpous (see p. 30); in *Macrolepiota* and *Chlorophyllum*, it is hemiangiocarpous (see p. 30).

4. *The annulus superus.* This organ has, as receptacle, first been distinguished in the *Phallales* (*Gastromycetes*) where it has no velar character. However, Lohwag (1926) showed convincingly the homologies of the organs of *Phallus* and *Clathrus*, *Dictyophora*, and other Phalloids with such agarics as *Amanita*. It turns out that we have reason to consider the so-called annulus superus, or apical veil (Lohwags « Manschette ») as corresponding to the receptacle of the *Phalloideae*. It is not an annulus of the kind that was discussed under the term of « marginal annulus » above nor is it part of the volva, but rather is it formed under pressure of a volva against the pileus and herewith against the hymenophore growing into the covering tissue of the young apex of the stipe. Such outgrowths of palisade structures against dense tissue tend to be pseudoparenchymatic and if tramal elements are involved, partly pseudoparenchymatic according to Lohwag, and others. The « annulus » of the Amanitas is, indeed, mainly composed of isodiametric and inflated elements. Limiting ourselves to the agarics, we, consequently, distinguish the apical

veil or annulus superus from other annular formations by its origin which is not marginal nor volval but hymenophoral. It may be suspected that some smaller or larger portions of certain annuli in the agarics (e. g. *Stropharia coronilla*) belong to this category but since the apical veil can, a priori, exist only in a volvate species where the margin is not strongly enough incurved or convex to separate most of the hymenophore from the stipe, the chances are remote. The typical example of an annulus superus is *Amanita caesarea* and its relatives.

The above categories do not seem to be immediately applicable to all velar formations It is not fully proved that all the annular formations of the boletes are actually marginal annuli as long as their development has not been studied. Many velar formations are still puzzling, even if some ontogenetic hypothesis is temporarily admitted. We do not know exactly what to think about the annulus of *Chamaeota* and many other genera. In other cases, as was to be foreseen, the annulus is complex and its formation is partly that of one category of veils, and partly that of another.

However that may be, it is considered to be a wise course to continue using the general terms annulus and veil in the original sense where a closer interpretation would be mere guesswork.

The presence or absence of volva, pellicular veil, cortina, marginal veil, or apical veil (annulus superus) is not in itself, i. e. unless accompanied by correlated characters, a decisive character for taxonomic purposes. Very natural groups such as *Suillus* among the *Boletaceae* and *Russula* and *Lactarius* among the *Russulaceae* contain species with well-developed marginal veil and some without any veil, and the veiled forms are often more closely related to evelate forms than to other veiled forms. This is especially easily demonstrable in *Suillus*, sect. *Granulati*, and in *Russula annulata* (that has an evelate form). It is well known that *Amanita*, without any appreciable hiatus grades from forms with well developed volva into such with friable volva which is often obliterated; and forms otherwise closely allied to each other, in the *Agaricaceae*, either have or lack a volva. The annulus superus is rather inconstant in certain species of *Pseudoamanita* (subgenus of *Amanita*) and *Vaginaria* (subgenus of *Amanita*), e. g. *Amanita gemmata* and *A. fulva*. In the genus *Gymnopilus*, closely allied species are distinguished almost exclusively by the presence or the absence of the cortina.

On the other hand, some significance should be conceded to the

veil especially on the species level in spite of the fact that in some particular cases (the amanitas named above, *Russula annulata*, *Agrocybe praecox*, and even *Suillus brevipes* and *S. Grevillei*) this character is not useful for the distinction of species. It can also be used in order to dispel ancient superstitions such as the alleged close affinity of the *Agaricaceae* and the *Amanitaceae* because of the presence of the annular veil wich has been established as of essentially different origin.

In a few cases, the anatomy of the veil has some significance, e. g. in the intrageneric taxonomy of *Gomphidius*, and possibly, in future investigations on the Amanitas.

II. THE SPORE PRINT

The only macroscopical character available that concerns the basidiospores in the *Agaricales* is the color of the spore print. This was first emphasized in a classification by Fries. However, Fries minimized (using words like «sordidae» for the description of the spore color), overlooked, or merely ignored certain complications that make it impossible to use his classification, even for an artificial system, without introducing important modifications.

1. *The green spored group.* This group of agarics, considered as a taxonomic unit in some artificial classifications, belongs in various families and genera in the *Agaricales*, viz. the *Agaricaceae*, *Amanitaceae*, probably the *Tricholomataceae*, and the *Boletaceae*. The green spored group has no place in the Friesian classification because Fries misinterpreted either the spore color (in *Phylloporus*), or the species (all the tropical green spored agarics); it has no place in the modern classification because it contains elements from four different spheres of affinities.

2. *The pink spored group.* In spite of the combination by Fries of the pink spored agarics in one group and the pink spored boletes in another, the former is not a homogeneous taxonomic group. The two largest constituents are *Rhodophyllus*, and the *Pluteae*. The former group belongs in the large family *Rhodophyllaceae*, and the latter in the family *Amanitaceae*, none of them related to the other. Fries, and the key writers following him, especially Saccardo, paid no attention to the fact that there are many other agarics with pink spores, and in order to get to the right genus, in their schemes, it is necessary,

as is so often the case, to assume the spores to be white rather than pink. This holds true for such genera as *Rhodocybe* (*Rhodophyllaceae*), some species of *Clitopilus* (al.), *Phyllotopsis*, *Schizophyllum*, several common *Collybiae*, one or two species of *Amanita* and the *Agaricaceae* (*Leucocoprineae*).

3. *The yellow spored group.* There are numerous species in several genera of « white spored agarics » and « white spored boletes » (the latter term is superfluous since no such thing exists) that have yellowish cream colored to ochraceous or citrinous spores but have passed as white spored because of errors of observation. Part of the error of the observation was due to the fact that in obtaining the spore print, the piles were formerly (and still are according to the recommendations of recent books) put over black or blue paper, the latter in the erroneous assumption that this color did not occur in basidiomycete spores. In order to discover pale colors which are easily misinterpreted as white on a dark background, it is necessary to use paper as pure white as is used and recommended by Crawshay (1930). This is also true for the paler tints of pink.

4. *The black spored (« melanosporous ») group.* This group intergrades with the brown and purple spored groups at certain levels, as has been recognized by Britzelmayr and other earlier writers. The Friesian *Melanosporae* fall now entirely into the *Coprinaceae* with the single exception of the genus *Gomphidius*, which belongs in the *Gomphidiaceae*, near the boletes. Even *Lacrymaria*, once wrongly incorporated into the purple spored group by Fries, is now considered as belonging to the *Coprinaceae*.

5. *The brown spored (« ochrosporous ») group* is not a homogeneous group as was anticipated by Fries. Some genera, in their present, narrowed sense, come close to, and form a parallel series with the *Stropharia-Naematoloma-Psilocybe-Deconica-Melanotus* group, a series so closely related that it is often difficult to separate the corresponding genera and sections of both series. Another series parallels the *Coprinaceae* in a much less strict manner, and has since been separated from the other *Ochrosporae* as a family by itself, the *Bolbitiaceae*. It differs from the *Cortinariaceae*. In the *Cortinariaceae* we have again two parallel series, already partly recognized by Fries: one contains the genera with argillaceous fuscous spore print such as *Inocybe* and *Hebeloma*, the other the genera with vividly rusty colored spore print such as *Cortinarius* and *Gymnopilus*.

The above examples show that the spore print colors are not as

such, and in themselves, indicative of an affinity between groups according to general classes of colors (white, pink, purple, black, brown, etc.). They can be used on the family level only if modified by other correlated characters, and only on a lower level can they be used as the leading characters of taxonomic groups. This shows that Fries' discovery of the spore print colors as a taxonomic character of first grade importance was certainly a fortunate and valuable contribution to the systematics of the *Agaricales*, however it should be used with reason, without generalizations, and never in a spirit of dogmatic schematism.

The colors observed in fresh spore prints are apt to change in the herbarium due to farther dehydration, and in some cases they loose the olive hue, so characteristic for the spore print for several genera of the *Boletaceae*, in other cases they bleach to almost white, after having been a distinct vinaceous pink in some species of *Tylopilus* (*Boletaceae*) while in *Russula, Melanoleuca, Cantharellula*, and other « white spored » agarics, the pale colored fresh spore print eventually darkens to decidedly cream color or ochraceous, especially if prepared with some fixative. In *Gomphidius* the deep fuscous or olive-black spore print becomes deep rusty brown in a few years of preservation. Since many tedious observations by the author (1945 1946) have shown that the taxonomically important differences are found in the fresh non-dehydrated spore prints, it is necessary to identify the color immediately with the help of a good color chart [1]. The pale

[1] Many mycologists, unfortunately, do not use charts at all but rely on color terms that do not mean the same thing to other people, especially when translated into foreign languages. Some still use Oberthuer, or Klincksieck, but the majority uses Ridgway, *Color Standards and Color Nomenclature*, Washington, D. C. 1912. This book is now difficult to obtain, and besides has the disadvantage of being subject to drastic color changes in the plates after some time of exposure to light. Therefore, many scientists use a newer chart, Maerz, A. and M. Rea Paul, *Dictionary of Color*, New York, 1930. The plates are said to be light resistant, and besides the number of colors shown is larger than in Ridgway, especially in some colors frequently found in *Agaricales*. The richest and most vivid colors of spore prints, such as those of *Gymnopilus*, are nevertheless often hard to match in any color chart, and until a special chart for these tinges is published, the mycologist will do well to get the nearest approximately corresponding number, adding « deeper », or whatever the difference may be. The spore prints between pure white and deep ochraceous, such as found in the *Russulaceae, Melanoleuca, Drosella*, etc. should be compared with Crawshay's plate (Crawshay, *The Spore Ornamentation of the Russulas*. London 1930).

tints should be rigorously observed on paper of the whiteness of that used in Crawshay's (*l. c.*) plate; the discussion of even whiter ground colors (salts, etc.) is rather theoretical than practical.

III. THE MYCELIUM

A. *Cultural characters*

The mycelium has not been used thus far for taxonomic purposes on a large scale. It is obvious, however, that differences of color, zonation, consistency and manner of growth in standard cultures, as employed for *Porias* by Baxter should also be of diagnostic value in the *Agaricales*. We know that some species of *Agaricales* have luminescent mycelia. There is now available a rather long list of agarics with luminescent mycelia, a character with certainty demonstrable only in laboratory cultures. Some species have mycelia with a characteristic odor. This character can be used for the determination of ectotrophic mycorrhiza. The mycorrhiza of *Russula punctata* and *R. Dudmanii* has a characteristic odor of iodoform which can be obtained in test tube culture.

Some mycelia form sclerotia (see under B.), rhizomorphs (see under B), oidia (or what is called so in the literature on life cycles and sexuality of the *Basidiomycetes*), conidia, chlamydospores (or chlamydosporoid oidia), oleiferous hyphae (see chapter IX), and even mycelial basidia, and mycelial cystidia. The latter have been named allocysts by Kuhner, a term that should be accepted in view of the original definition of the word cystidia. These allocysts often resemble the cystidia or cheilocystidia of the hymenophore of the same species, or of allied species, but in other cases, they do not remind one of any analogous bodies in the carpophores. All these characters will undoubtedly be used for taxonomic purposes as soon as more data become available. The main difficulty here arises from the variance of conditions necessary to grow mycelia of *Agaricales*, and even so, the mycelia are often short lived and obviously not in normal growing condition. Under these circumstances, a standard method that makes cultures possible and comparable for taxonomic purposes cannot yet be indicated. Most non mycorrhizal fungi can be grown on malt agar and on Lütz' synthetic medium, also in liquid media of analogous composition. A widely applicable medium has been indicated by

Kuhner, and it has been tested, along with many other media, by the author. It is a modified Lutz medium [1], which appears to be suitable for almost all non mycorrhizal species and many mycorrhizal species of the agarics and boletes. The cultures can be started from spores, from the internal tissue of the pileus or stipe, or from the hymenophore (hymenium plus subhymenium). The separation of the pieces to be inoculated should be made under binocular in order to avoid infected places; the interior of young and fresh carpophores is safest in regard to possible contamination. Bacterial contamination is most difficult to avoid in many cases, and separation of the fungus mycelium from the bacteria is not always possible. The culture methods indicated above cannot be applied to certain species of *Amanita* and certain boletes and *Gomphidius*, certain *Cortinarii* and *Russulaceae*. Their culture requires special techniques, e. gr. sterilisation by filtration through a bacterial filter (Seitz or Berkefeld), addition of growth substances, root extracts, etc. In a few cases, all attempts at culturing have thus far been unsuccesful.

A pure culture is also necessary for studies on the sexuality of the *Agaricales* (see chapter XVI). In this connection it is often necessary to start from a single germinating spore, and later confront the resulting primary mycelia. As for the technique involved, the reader is referred to Vandendries's papers (see literature); some interesting technical information can also be found in Kuhner's *Recherches morphologiques et caryologiques...* (1946).

[1] The formula used by the author :

Water	1000	gr
Difco agar	25	»
Vitrums Maltextrakt (Stockholm)	10	»
Ammonium nitrate	1	»
Ammonium phosphate	1	»
Magnesium sulfate	0 1	»
Ferric sulfate	0 1	»
Manganese sulfate	0 05	»

As has been pointed out by A. B. Hatch & C. T. Hatch (*Journ. Arnold Arb.* **14**: 325. 1933), the American brands of malt extract are not suitable. The brand obtained from Apoteksvarucentral, Stockholm, Sweden, proved to be superior to American brands in all cases.

B. Characters observed in nature

On the base of the stipe or the point of attachment of the pileus to the substratum, a tomentose or strigose or silky arachnoid mass or mat of hyphae is observed in many species; in others, white or colored strands of hyphae are macroscopically visible and can be followed through the ground or substratum. In the first case, these mycelial formations are called mycelial tomentum, or basal tomentum; in the second case, they are known as rhizomorphs. In both cases, they are frequently useful characters for the systematist, especially in the *Gomphidiaceae*, certain *Agaricaceae*, *Boletaceae* and *Tricholomataceae*. A special form of mycelial tomentum formed in advance and independent of the formation of carpophores is the *Ozonium* of *Coprinus radians* [*].

The mycelial tomentum differs mainly in color, according to the species or variety; also in the degree of development and in consistency.

The rhizomorphs can be subdivided into:

1. True, eventually black, rhizomorphs, and
2. White mycelial strands.

Though admitting that rhizomorphs are usually constant specific and perhaps sectional characters, one will agree with De Bary who says (1887, p. 22) «that the formation of strands is not necessarily found in all the species that belong to the cycles of affinity indicated by their family and generic names]; on the contrary, it may be wanting in one of two nearly allied species, and be found in the other».

Other formations of the mycelium are the pseudosclerotia, sclerotia, perennial pseudorrhizae, cryptas, mycorrhizas, and sterile carpophores. The latter will be discussed in subsequent chapters since they are rather a modification of the seasonal basidiocarpous formations, whereas the others are not in any way homologous with the carpophores, and can rather be characterized as special organs where primary functions are either long term resistance, storage of food material, exchange of nutrient substances with the rootlets of the

[*] Excepting the *Ozonium*, we can synonymize the mycelial tomentum with Fayod's « mycelium secondaire » or De Bary's secondary mycelium.

mycorrhizal symbiont. In the first category belong: black rhizomorphs, in the second — sclerotia, perennial pseudorrhizae, and in the third — the cryptas and mycorrhizae. The pseudosclerotia are probably without function, and merely a result of processes of extracellular assimilation of substratum with a certain dense hyphal growth in a well circumscribed sphere of the mycelium.

There are, therefore, the following three groups of mycelial formations:

1. *The pseudosclerotium.* This is a mass of substratum (mineral or humus particles, or wood) held together by the mycelium so as to form definitely circumscribed bodies resembling sclerotia. Such formations are characteristic in *Polyporus tuberaster*, *Phlebopus colossus*, *Panus velutinus* (Pl. IV).

2. *The sclerotia, perennial pseudorrhizae, and the black rhizomorphs.* The sclerotia differ from the pseudorrhizae and rhizomorphs in shape. The sclerotia are usually bulbous or ovoid-ellipsoid to globose bodies, either immersed or superficial; the perennial pseudorrhizae are root-like hypogaeous bodies which are vertically elongated; the black rhizomorphs are horse-hair-like filaments. Sclerotia are found in *Pleurotus tuber-regium* (Pl. III) where they are very large, in *Lentinus tuberosa* (medium sized), and in three *Collybiae* where they are small.

Sclerotia (mycéliums persistants tuberculeux) have been subdivided by De Bary (1884) and Fayod (1889) into mycelial tubercles, exosclerotia, and endosclerotia. The latter has not yet been found in *Agaricales*. However, the first two types are represented in this order. Mycelial tubercles are those sclerotia «where one can oppose to their morphological base, one or several points from which the stipes of the carpophores rise at germination» (Fayod 1889). As an example of this kind, Fayod indicates *Collybia tuberosa*. In the exosclerotium, no such points of germination are present, and any cell or group of cells in the cortical layer of the exosclerotium is apt to produce carpophores; yet, their morphological base (the «hilum» end) is usually recognizable all through its development. Such a sclerotium is formed by *Coprinus stercorarius*, *Collybia racemosa*, and *C. Cookei*. It is surprising to find both types represented in one single section of *Collybia*.

Perennial pseudorrhizae have been studied by Buller (1934). They represent the perennial base of the annual pseudorrhizae of the carpophores branching (underneath the earth and close to or inside the substratum, into several individual carpophores. A special term

for the annual pseudorrhiza is necessary since the latter is merely a subterranean (or submerged) part of the carpophore, more precisely of the stipe, and often exists alone, directly rising from the mycelium rather than from the perennial pseudorrhiza. Neither the perennial pseudorrhiza nor the annual pseudorrhiza should be confused with the rhizomes of higher plants with which they are not homologous (though analogous in several respects).

The strange short-lived, soft, sclerotium-like body from which *Tricholoma sclerotoides* Morse is said to arise, is neither quite comparable with any well known type of sclerotium, nor is it comparable with the similar formations known in *Rhodophyllus abortivus*. They may temporarily be kept in a separate group without a definite term.

3. *Cryptas* are sleeve-like formations around tree roots (especially *Coffea*, *Citrus* and other trees of the evergreen kind) in tropical and subtropical countries. These organs of the fungus provide shelter for certain scale insects between them and the roots and rootlets of these trees. They are the morphological expression of a strange and highly complicated coexistence of various organisms, living partly in epibiosis, partly in symbiosis, and partly in a parasite-host relationship.

Mycorrhizae are more tender structures consisting of mycelial hyphae enveloping only the thin rootlets and root hairs of certain trees, mainly conifers, *Salicales*, *Fagales*, *Urticales*, *Columniferae* (mainly *Tilia*) and *Ligustrales* (mainly *Fraxinus*)[1]. More precisely, they should be referred to as ectotrophic mycorrhizae. The mycelium of roughly one half of the species of *Agaricales* may be considered as potentially mycorrhiza-forming. This figure is the result of a rough calculation on the basis of syntheses made between fungus and tree in laboratory experiments plus a cautious generalization for the taxonomic groups involved insofar as field observations confirm an ecologic situation similar to that found in experimental studies with closely related species. It is probable that the situation in the tropics differs slightly from that in the temperate zones with the non-mycorrhizal fungi possibly favored under tropical conditions. In ectotrophic mycorrhiza, the phanerogamic symbiont may be furthered in certain phases of its development by the association but it can also be grown — or can grow in nature — without interference of the fungus sym-

[1] In some other families, mycorrhiza is also found but it is highly doubtful that the fungus species involved belong to the *Agaricales*. At least no data supporting such a relationship are available at present.

biont. The fungi, however, in a large number of cases, do not seem to be able to develop normally unless the connection with the phanerogamic symbiont is established, i. e. unless mycorrhizae are formed. The fungi forming the ectotrophic mycorrhiza of this type are often highly specialized. This specialization of the ectotrophic mycorrhiza gives into the hands of the mycologists an additional character comparable to that available to the student of parasitic fungi of certain groups such as the *Uredinales* and *Exobasidiales* among the *Basidiomycetes*. It must, however, be kept in mind that laboratory experiments neglecting the specific soil conditions and microfloristic features (competition) of the natural habitat tend to obscure rather than elucidate the question of specificity of a given fungus whereas field observations, especially if made with insufficient skill or care, are often inaccurate or inconclusive, or else too limited in their purely regional importance. It has been emphasized by Melin (1936) that field observations are very important and desirable as an indicator for the planning and setting of further experimental study ; the same may be said for taxonomy. There is undoubtedly a connection between taxonomic problems and specificity of fungus symbionts as to their mycorrhizal hosts. A temporary tendency to determine this relationship with geobotanical methods (Zinserling, 1922-1924) may be interesting for ecologists but it does not help materially to make field observations on mycorrhiza relationship more precise. A single coniferous tree, even a seedling, in a broad leaved stand is apt to alter locally the aspect of the myco flora as expressed by the population of carpophores within a circle with a radius slightly larger than the spread of the root system (i. e. up to 30 ft.) ; herbaceous species of *Salix*, *Betula* and *Quercus* as well as seedlings of larger trees are often overlooked in stands of more conspicuous but different trees, and wrong conclusions are likely unless a careful survey of all plants of a given locality and a comparative study of other corresponding localities is made.

Agaricales are also involved in another kind of mycorrhiza, the so-called endotrophic mycorrhiza where the hyphae of the fungus enter the tissue of the roots, and are assimilated by the plant. In some tropical orchids, it has been shown that the fungus hyphae belong to agarics such as *Armillariella mellea*, *Micromphale javanicum* and probably *Gymnopilus aculeatus*. In these cases, the orchids are as dependent on the presence of the fungus as, in ectotrophic mycorrhiza, the fungus is dependent on the higher plant, and ger-

mination can be achieved under ordinary laboratory conditions only after a synthesis of fungus and seed. On the other hand, the fungi named above are by no means dependent on the orchid for their normal development, nor are they in any way specialized as many of the ectotrophic mycorrhizas are. For example, *Armillariella mellea* is almost cosmopolitan and grows abundantly as a wood parasite and also saprophytically in wide boreal areas where none of the mycorrhizal orchids occurs. The same is true for *Micromphale pacaanum* and *Gymnopilus aculeatus* which are subtropical tropical species, yet not specific for orchids but growing on all kinds of *Monocotyledones*, either as symbionts, or as parasites, or as saprophytes, mostly the last.

IV. NON BASIDIOCARPOUS CARPOPHOROIDS AND ABORTED CARPOPHORES

Sterile bodies that have no visible purpose but are formed the same way and under similar conditions as the normal basidia bearing carpophores have been observed in *Agaricales* of various groups. They are here called carpophoroids. The only explanation of these strange, apparently function-less bodies is that of an atavistic aberration whereby a gastroid form is occasionally maintained in normally gymnocarpous or hemiangiocarpous or pseudoangiocarpous species, which often leads to sterility. We have such an example in *Boletus rubellus* ssp. *caribaeus* which is evidently comparable to the fertile gastroid forms observed in *Boletinus decipiens* but has never been seen to form basidia or spores. In this case we observe that the carpophore fails to ever achieve the last stage of its individual development after it once, probably exceptionally, reached its angiocarpous phase. These aborted individuals are, however, rather rare and usually constitute only a small percentage of the total local population.

On the other hand, there are several examples, where sterile masses of carpophoroids are formed regularly either by a large percentage of the local population of a species, as in *Rhodophyllus abortivus* (Pl. VI) or the abnormal fruiting bodies completely replacing the normal basidiophorous form on a local scale, as in *Panus tigrinus*. Further investigation of these forms, especially in culture, and a study of their cytology may throw more light on them in the future. The abnormal, sterile forms of the species named above are so distinctive

that apparently they were considered taxonomically different from the normal carpophores by some mycologists. In fact, authentic specimens as well as the type collection of the type and only species of the genus *Acurtis* prove that *Acurtis* is the carpophoroid form of the *Rhodophyllus*, not a clavariaceous genus, just as *Lentodium* is the carpophoroid of *Panus tigrinus* rather than an independent genus. In the latter, the hymenophore is transformed into an irregular hyphal mass through which elongate holes run in all directions (reminiscent of the gleba of some gastromycetes). The author has seen only completely sterile forms of this aberration, and in this condition, it may properly be called a carpophoroid. Other authors indicate spore formation in the aborted hymenophore. In this case, the phenomenon appears to belong in the same category as the other common anomalies in agarics such as the pore-bearing forms of *Agaricus*, *Clitopilus*, etc., the so-called *Ptychella* forms, and many other aberrations which do not occur regularly with the normal carpophores, nor do they ordinarily form entire populations. The *Lentodium* form of the *Panus* is in a sense intermediate between an ordinary anomaly and a typical carpophoroid. However, even in typical carpophoroids as in the *Acurtis* form of *Rhodophyllus abortivus*, transient forms are occasionally observed. These show a pileus and a stipe and a zone that must be considered as hymenophoral. In this zone, sometimes occasional spores can be found, some of them formed on basidia, others directly from hyphae; in both cases, they tend to be thin-walled. The fibrillose, white outer layer of the carpophoroids tends to break off in these intermediate forms, and assumes the character of a «general veil», resembling a rudimentary peridium. These observations seem to leave little doubt but that these carpophoroids or *Acurtis*-forms of *Rhodophyllus* are actually gastromycetoid forms comparable to those of *Boletinus decipiens*.

Carpophoroids of a similar type have been observed by the author in a species of *Marasmiellus* from the Philippines, probably *Marasmius pandanicola* Henn., and closely related to *Marasmiellus semiustus* of the Neo-Tropics. Here, as in the *Acurtis*-form, many carpophores of a population are transformed into brain-shaped or amorphous sterile masses, much like those of the *Rhodophyllus* but less fleshy and smaller.

V. STILBOIDS

In other cases, the sterile, non-basidiocarpous formations with carpophore-like appearance have a definite function as propagula, and are not at all comparable with the aberrations named above. This is the case with the « gemmae » of what is described as *Omphalia flavida* Maublanc and Rangel[1], and has been studied by Buller (*Res. on Fung.* **6**: 387-443, 1934). Here, a sterile carpophore is formed that has a separable capitellum (« pileus ») which is blown by the wind from one leaf to another and thus serves for vegetative propagation, in this case of the epiphyllous phase of the life cycle of the fungus. The « gemmae » do not form any basidia but the capitella attach themselves to the leaf by their gelatinosity and the hyphae start immediately to form new exogenous mycelium parasitic on the leaf. It is especially interesting to remember that certain species of *Mycena* and *Marasmiellus* — as has been shown by the anatomical studies of Kühner (1926, 1938) — have the stipe actually separable from the pileus by an intermediate zone of different structure. The carpophore-like bodies of *Mycena flavida* (*Omphalia flavida*) were misunderstood by Cooke who described them in a genus otherwise without any relationship with the *Agaricales*, as *Stilbum flavidum* Cooke. The term « gemmae » used by Buller, and the implication of abortion of the fruitbodies found in Maublanc & Rangel's account (*Bull. Soc. Myc. Fr.* **30**: 41, 1914), are both inadequate or misleading in view of the evidence at hand, and therefore the term stilboids is proposed.

VI. CONIDIAL CARPOPHORES — IMPERFECT FORMS

It is well known that conidial carpophores are frequently formed by *Ascomycetes* such as *Xylaria*, and *Aphyllophorales* such as *Ptychogaster*. The controversial genus *Lycoperdellon* may be an example of a conidial fructification of a gastromycete. In the *Agaricales*, no such examples were known until now unless one would see an instance of conidial fruiting bodies in those specimens of *Asterophora* (*Nyctalis*) where the basidiospore production is (almost) entirely suppressed in

[1] This species, according to the descriptive data available, belongs to the genus *Mycena* although the spores are nonamyloid.

favor of chlamydospores. However, in this case, no modification of the carpophore is observed, and a hymenophore, potentially apt to produce basidia and basidiospores is always formed although sometimes in rudimentary form.

Yet, in recent observations, the author has been able to discover a typical instance of modified conidial carpophores in an agaric of the mountain region west of Tucuman, a new species of the genus *Armillariella*, *A. ditopa* Sing. ined. (Pl. XXIX). This species, before forming the basidiocarpous fructifications (which do not develop except under optimal temperature and moisture conditions) develops a simple clavarioid carpophore, entirely white and mealy from the innumerable arthrospores formed in palisadic chains on the surface of the clubs. The anatomical and cytological study of the corresponding stages reveals that they belong to the same organism; the arthrospores are binucleate and consequently belong to the dicaryotic phase, as do the carpophores with basidiospores. The arthrospore formation continues on the stipe of the basidiocarps, and the arthrospores formed there are equal, in every regard, with the arthrospores of the conidial fructifications. It appears that the conidial fructifications are homologous to the stipes of the basidiocarpous fructifications. Under certain circumstances, especially after severe changes of the meteorological and microclimatic conditions in certain seasons, it is possible to observe the conidial and basidiocarpous fructifications together, rising from the same dicaryotic mycelium.

The term arthrospores is here used in the sense of Langeron. The chains are radiately arranged when observed in a cross section of the conidial fructification, and consist of hyphae which soon become densely septate and fall apart at the septa in an irregular manner, the resulting spores being consequently what is often called «oidia» of a rectangular to ellipsoid shape, the majority ellipsoid. They are much broader than the basidiospores, and also slightly longer.

Whether the *Sclerostilbum* form of *Collybia racemosa* is another instance of conidial carpophores, or a young stage, cannot be decided at present.

VII. BULBILLOSIS — RHACOPHYLLUS FORMS

In rare cases, the carpophore of the *Agaricales* is sterile in the sense that sporulation is suppressed, yet the function of the basi

dium is maintained by the formation of bulbils. These are terminal members of the subhymenium which become more or less isodiametric and more or less sclerotized. The bodies bearing bulbils, are consequently neither carpophoroids nor stilboids, nor true carpophores. They are called *Rhacophyllus* forms and the phenomenon referred to is known as bulbillosis of the agarics. For more information on bulbillosis, see p. 104. and in the special part.

VIII. DEVELOPMENT OF THE PRIMORDIUM OF THE CARPOPHORE

It was Patouillard's conviction that all the carpophores [1] now usually classed as *Aphyllophorales* — i. e. his Aphyllophoracées — are gymnocarpous, consequently he named them « Gymnocarpes », and opposed them to the « Hemiangiocarpes » (virtually the *Agaricales* and the « Angiocarpes » (virtually the *Gastromycetes*). It is still true that, with one or very few exceptions, the *Aphyllophorales* must be considered as gymnocarpous. The *Gastromycetes* are mostly angiocarpous and only a few of the species approach the hemiangiocarpous type of development by becoming naked in a comparatively earlier stage, yet the shape of the hymenophore (gleba) is not such as to facilitate the discharge of the spores in the way of the *Agaricales*, and one is justified in letting them pass as basically angiocarpous. In some gastromycetes, the early stage of the hymenium is naked in the primordia and later becomes typically angiocarpous. For this form of ontogenesis, no special term has as yet been proposed. Consequently, the assumptions concerning the development of the *Aphyllophorales* and *Gastromycetes* as made by Patouillard are still mainly sound. It is in the *Agaricales* where he erred by generalization. It is, as has now been shown by Kuhner, and various other authors, not true that all, or even a large majority of the *Agaricales* are hemiangiocarpous. We now distinguish in this group four different types of individual development of the carpophores in regard to the position of their hymenium:

1. *Gymnocarpous*. The common type of development in *Russulaceae*, most of the *Boletaceae*, in numerous genera of the *Tricholomataceae*

[1] The term sporophore, frequently used in the sense of carpophore, is here rejected because it was first used for the basidium by Berkeley.

(*Rhodopaxillus*, *Leucopaxillus*, *Mycena*, etc.). Here, the hymenium is formed on the outside in the very earliest stages and remains so all through the stages of development.

2. *Pseudoangiocarpous.* The primordium has initially naked hymenial surface which later becomes internal by the incurving of the margin, and, at maturity, becomes exposed again by the expanding of the margin. This type of development is found in the veiled *Russulaceae* and *Boletaceae*, also in the veiled *Lentineae* (*Tricholomataceae* etc.).

3. *Hemiangiocarpous.* This type of development is common in the dark spored agarics, especially the *Strophariaceae*, and also in the *Amanitaceae*, probably most or all *Cortinariaceae* and *Agaricaceae*. The primordia have the hymenium formed on the inside, even in the earliest stages, and later become naked, approximately at maturity.

4. *Angiocarpous* (= *endocarpic*) Here, the fruiting bodies are either permanently angiocarpous (e. gr. the gastroid forms of *Boletinus decipiens*) (Pl. XXV, 5) except perhaps for the very earliest stages of the primordia, or they expose the hymenium by longitudinal rather than horizontal scission well after the first spores have attained maturity (as in *Galeropsis*).

The direction and the limitation of the hymenium in the course of development has also been studied by various authors, e. gr. by Kühner (1926), in the small and undoubtedly natural genus *Lentinellus*. The results are thus far not encouraging for the taxonomist: they show two opposed types of development within this same genus.

However, the internal or external development of the hymenium, and the variants of these two types, as described above, seem to have a distinct correlation with other important characters, and should not be neglected. On the other hand, lack of sufficient data on important species, even genera, makes premature conclusions rather dangerous.

IX. STRUCTURE OF THE CONTEXT OF THE CARPOPHORES

In most true *Agaricales* it is possible to distinguish two kinds of tissue which are called (according to Fayod, 1889):

1. The fundamental tissue, and
2. The connective tissue.

Ordinarily, i. e. in the homoiomerous [1] structure, the fundamental tissue consists of hyphae rather than of sphaerocysts; these hyphae are broader, firmer, and straighter than those of the connective hyphae but there is no fundamental difference as to their filamentous character which is the same in both kinds of tissue. This latter structure is typical for all families of the *Agaricales* except for the *Russulaceae*.

In some forms the fundamental hyphae are strongly thick walled, sclerotic, and tough, thus showing the anatomical basis of the « tough » to « leathery » consistency of the carpophores of certain species, or genera. However, the relative thickness of the wall is not by any means a direct measure of the relative toughness of the carpophores. *Trogia cantharelloides* has rather uniformly but moderately thickened hyphal walls, yet, the carpophores are definitely tough and reviving, whereas *Pleurotus ostreatus* has a majority of rather strongly thickened hyphal walls even in the hymenophoral trama, but is generally described as fleshy and putrescent rather than tough and reviving. The string- or horse-hair-like appearance of the stipes of some species of *Marasmius* and *Micromphale* is due, in addition to the thickness of the walls of the cortical hyphae, to an intimate coherence of the hyphae which are often plugged into each other by means of alternating thorns or spurs fitting into a depression in the neighboring hyphae.

In certain species, the connective tissue is absent, and here we have reason to suspect that we deal with agaricoid forms of lower groups, e. g. in *Cantharellus cupulatus* Fr., as was pointed out by Kühner (1945) who refers to this species as *Omphalia rustica*. It may, however, be wiser to not include the character of differentiation of the tissue into the diagnosis of the *Agaricales* because it is perfectly possible that a reduction of the connective tissue in certain reduced forms does not necessarily mean that these species have no affinity with other *Agaricales*, especially if a well developed subhymenium is present. On the other hand it is often observed that the fundamental

[1] The terms « heteromerous » and « homoiomerous » are also used in lichenology, in a broader sense, yet they have a similar meaning. The alternative terms « heteromorphous » and « homomorphous » have been used for fungous tissues composed of identical and different elements respectively and cannot therefore be employed for this particular case of heterogenity; they are, at present, used preferably for the characterization of the hymenophoral edges as compared with that of the remaining part of the hymenium (see p. 46).

hyphae are either transformed into a pseudoparenchymatic tissue, or replaced by vascular hyphae.

For instance, in the *Russulaceae*, the fundamental tissue is very well differentiated from the connective tissue because it consists almost entirely or entirely of « nests » of sphaerocysts (Pl. XIX, 5). This structure has also been observed in certain gastromycetes (family *Astrogastraceae*, as it is called by Malençon and Heim). It is called heteromerous by G. Beck (1922).

Generally speaking, the tissue of the stipe is usually somewhat denser and more fibrous or cartilaginous, at least in parts, than that of the pileus and the hymenophoral trama, and a sudden transition from the tighter packed hyphae of the stipe to the looser tissue in the pileus may account for what is often described as « pileus and stipe non continuous », or « distinct », or « separable ». There is, however, rarely a sharp line between continuous and discontinuous stipes in the *Agaricales*, and this character is neither constant nor particularly helpful for determination in most instances. The only case where the separability of the stipe from the pileus is at present applicable with a definite anatomical meaning, is that discovered by Kühner (1926) in *Mycena and Marasmiellus* where a separation layer consisting of hyphae of a different kind is imbedded between the longitudinally arranged hyphae of the stipe and the larger spreading hyphae of the pileus. The separation layer is probably homologous with the layer separating the stalk and the head of the stilboids in *Omphalia flavida*. It can be used as a specific and sectional character.

In many species we find zones of the context or the entire context gelatinized, i. e. the hyphal walls produce a gelatinous matter into which they are finally imbedded and by which they are separated from each other (Pl. XIX, 1; XX, 4). In typically gelatinized tissues, the hyphae of the gelatinous zone are immediately recognizable in 10 % KOH mounts by their strikingly loose arrangement, and as a rule, they are thin, and have thin walls and clamp connections *. There is, however, no sharp delimitation between gelatinized and

* The mucus forming the gelatinous mass can, in case of doubt, be easily demonstrated by Kühner's method (1933): Dye the sections during several minutes in watery solution of cresyl blue where the walls of the hyphae take a beautiful violaceous or mauve color but the mucilage remains colorless; one differentiates subsequently in absolute alcohol which dehydrates them at the same time and permits the dye to be fixed on the mucus; to stop the differentiation it is sufficient to pass the sections through xylol; the mucus is then blue

non gelatinous tissues, as can be noticed more readily if the gelatinosity of the surface layers of pileus or stipe are studied. We shall see that there is not just a glutinous pileus (with hyphae scattered in the mucus) and a dry pileus, but all kinds of transitional conditions are seen. The same is naturally true about the gelatinosity of the context. Many tissues consisting of thick walled hyphae produce a slight amount of gelatinous matter and the hyphae are moderately densely arranged. These tissues are interpreted differently by different observers [16].

One whole tribe in the *Tricholomataceae*, viz. the *Resupinateae*, and several genera such as *Dictyopanus* and *Phaeomyceua* have partly gelatinous trama. The tissue of most typical *Boletaceae* is, to a certain degree, gelatinized which accounts for the soft, succulent context characteristic for most representatives of that family as well as related families. A distinct gelatinous layer is also observed in some species of *Crepidotus* (*C. mollis*, *C. uber*, etc.), so conspicuously so that such an astute observer as Patouillard, misinterpreted a very old specimen of a tropical *Crepidotus* as a tremellaceous species with holo basidia, and described it as new genus, *Tremellopsis*, belonging allegedly, in the neighborhood of *Sparassis*.

Another interesting structure involving the fundamental and the connective tissue, is that of *Amanita* and related genera of the *Amanitaceae*. Kühner who justly gives credit to Boudier (1866) for having discovered it, describes it as follows : « In the Amanitas (and in the Limacellas)... the connective elements are assembled, end by end, into hyphae, as are the majority of the elements, the fundamental ones as well as the connective ones, in the other *Agaricales* ; the fundamental elements of the Amanitas and the Limacellas, however, especially those in the context of the stipe, are isolated and terminal at the tip of the ramifications of the connective hyphae » (Kühner, 1945, p. 162).

There are also other than fundamental and connective hyphae in the tissues of the *Agaricales*. They belong to the conducting system, and serve for the secretion and excretion of substances, and in a general way, the transport of substances in the carpophore. It is here as elsewhere impossible to always clearly separate these elements from others on a morphological and physiological basis, as it is

[16] Patouillard, Lloyd, and Singer considered the trama of *Filoboletus gracilis* gelatinized ; R. Heim (1946) thinks it is not.

obvious that in many instances the functions are not limited to the specialized organs, or else the specialized organs have often lost their original function.

Heim (1931) has not maintained Fayod's sharp separation between the « laticiferous » and the « oleiferous » type of conducting elements. Yet, it may be that Fayod's division is basically correct in spite of the fact that, chemically, they seem to intergrade. It would appear that what « laticiferous hyphae » there are in the Russulas, should, according to the Fayodian terminology, be called « oleiferous hyphae », and they are the ones that according to him originate in the connective tissue, and are continued into the « cystidia » of the *Russulae*. In *Lactarius* and *Mycena* the vessels carrying the latex are called laticifers in a narrow sense, yet the resinous substance responsible for the acrid taste of many *Russulaceae* is found localized in the « oleiferous hyphae » of *Russula* as well as in the laticifers of *Lactarius*, as can be demonstrated by the acrid taste of the latex in many *Lactarii*. On the other hand, there are *Lactarii* with mild taste and abundant latex. Fayod believed (though he was not certain about it) that the laticiferous vessels actually originate in elements of the fundamental tissue.

Leaving the morphological aspect aside for the present, we are inclined to admit a temporary classification of the types of vascular bodies on the basis of their function and known chemical and physical differences rather than on their supposed origin.

There would then be the following types to be distinguished

1. *The laticifers in the narrowest sense.* These carry latex, or are homologous to laticifers that do carry latex; they do not absorb cresyl blue, do not become deep blue throughout the interior, and they do not necessarily become deep blue in sulfovaniline or brown in formalin. They are not sieve like on the surface. Example latex carrying vessels of *Lactarius volemus*, or *L. nigroviolascens* (Pl. XVIII, 5; XX, 1).

2. *The oleiferous* [1] *hyphae in the sense of Fayod.* These do not carry latex, but often carry resinous substances associated with an acrid

[1] The word is somewhat unfortunate since it specifies the contents, yet the contents are complex and variable, and organic « oils » are certainly a minor factor, if at all. However, terms are only words with a definite scientific meaning, and their derivation should not concern us to the degree of proposing changes This is also the reason why the author is reluctant to give up the term germpore as was proposed by Locquin.

taste of the carpophores, and then they usually turn deep blue in sulfovanilline or brown in sulfoformalin or black in sulfobenzaldehyde. The type of oleiferous hyphae reacting with these aldehydes may turn out to be different from the non reacting types, yet we take them as being the same, as did **Fayod**. Examples : 1) of the non reacting type : *Amanita vaginata* (Pl. XVIII, 2); 2) of the type giving marked color reactions with acidaldehyde combinations : *Russula emetica*.

3. *The gloeo-vessels, in the sense of Singer (1945).* These are vessel like elements attached to gloeocystidia projected into the trama and staining deep blue. Example : *Favolaschia saccharina*. In the *Agaricales*, they have been observed in *Lactocollybia* (Pl. XVIII, 5). Perhaps, they are also latex carriers, since in the same genus, a laticiferous species that actually exudes a latex on bruising (*L. lacrimosa*) has been described.

4. *The coscinoids, in the sense of Singer (1947).* These are conducting elements of dark color with a sieve-like surface which is due to winding perforations and holes inside these otherwise solid filaments. The coscinoids (Pl. XVIII, 6) are found running through all parts and organs of the carpophores of *Linderomyces lateritius*, proliferating into cystidia-like bodies which are called coscinocystidia.

The fruiting bodies of some species are composed almost entirely of conductive elements, i. e. the structural function of the fundamental tissue has been taken over by the elements of the vascular system. Examples of this strange and rare condition are found among the *Tricholomataceae* (*Lactocollybia*) and also in the ochre-spored group (*Phlebonema*).

X. The hymenial layer of the carpophore

The Basidia

As compared with *Aphyllophorales* and the heterobasidial orders of the *Basidiomycetes*, the *Agaricales* are remarkable for the comparative uniformity of shape and development of their basidia. They are all holobasidia, i. e. constantly and persistently unicellular and not divided into what is described as « probasidia » and « epibasidia » (rather inadequate terms). Their position is always [12] in a palisade

[12] Kniep (1927) and others indicate mycelial basidia in *Armillariella mellea*; very little is known about their occurrence in other species and genera, and about their cytology as compared with that of the hymenial basidia.

characterized by the approximately even level of the basal septum and the acrogenous sterigmata, the former being the wall between the basidiophorous terminal subhymenial cell and the basidium itself, the latter — the connecting link between the basidium and the spore just before discharge of the latter (usually remaining on the old basidium until its collapse). In all *Agaricales*, the basidia are standing side by side (or intermixed with pseudoparaphyses), with their longitudinal axis parallel to the longitudinal axis of the neighboring basidia (provided they cover an approximately plane surface such as the side of a lamella). This special type of palisade is called hymenium. This term is not exclusively used in the *Basidiomycetes*, nor is it exclusively used for spore bearing surfaces. The apothecia of the *Pezizales* and related *Discomycetes* are covered with a similar layer consisting of asci, and, as will be explained later, the sterile surface of the carpophores of the *Agaricales* are frequently covered by a hymenium in which the basidia are only a small minority of the elements observed.

Most basidia are clavate or almost so, yet some show a strong ventricosity below the apex which is then broadly capitate and constricted beneath the capitellum, or cylindric to attenuate and broadly rounded at the tip. This latter shape would put them in the category of what is now called the *Urnigera*-type of basidia were it not for the number of sterigmata formed which is always 2 to 4 in these *Agaricales* whereas it is up to 8 in the *Aphyllophorales* with typical *Urnigera* basidia. This false *Urnigera*-type is often found mixed in with normal clavate basidia in the same carpophore, or else some carpophores have the false *Urnigera*-basidia while other individuals have all normal basidia (e. gr. in *Gymnopilus*). According to the author's observations on the nuclear divisions in *Gymnopilus*, this shape is closely connected with the level at which the spindles are formed, and probably a secondary expression of an abnormally low position of the nuclei at the reduction division. A special case of the false *Urnigera*-type is the *Godfrinia* type, first described by Maire for the two spored parthenogenetic form of *Hygrocybe conica*.

All *Agaricales* have chiastobasidia (see p. 96), a term mainly based on the cytology of the basidium, but the chiastobasidium is also characterized by its shape and development. It becomes more broadly clavate when mature, but is fusoid or narrowly clavate when young rather than cylindric filamentous. Besides, the chiastobasidium is, as a rule, less elongate than the stichobasidium. Within the chias-

tobasidial group, there is a large degree of variation as to the relative length of the basidia, thus absolute length compared with the absolute length of the spores, their absolute breadth in comparison with the length of ellipsoid spores, and the factor (F = length : width) of both dimensions of the basidia compared with the corresponding figure of the spores.

Generally speaking, the basidia of the *Agaricales* with ellipsoid or approximately ellipsoid spores, are about (or often exactly) as broad as the spores are long [1]. They are about two to five times as long as the longer axis of the spores, and if longer, they belong to a type that has some taxonomic importance because of its abnormal length. The abnormal length of the *Hygrophorus* basidium, causing the lamellae to be very thick and waxy in consistency, has been used as one of the characters of the family *Hygrophoraceae*. Some *Tricholomata*, some *Lyophylleae*, the genus *Catathelasma*, some *Mycenae* and *Omphalina umbellifera* along with closely allied species, also many *Amanitae*, are notorious for their longer-than-normal basidia, but they differ from the *Hygrophoraceae* in other regards. The genus *Laccaria* has thick lamellae but the basidia are not too long as compared with the size of the spores, and it is the thickness of the trama that is responsible for the thickness of the lamellae. The *Strobilomycetaceae*, among the boletes, are noted for their more voluminous hymenial elements, including the basidia, and *Agaricus*, on the other hand, is characterized by the very small size of the basidia as compared with that of the *Strophariaceae* and *Coprinaceae*. Short and thick basidia are characteristic for *Conocybe* (*Bolbitiaceae*).

The walls of the basidia are usually thin, and in old specimens and in poorly dried herbarium specimens, the basidia collapse soon after maturity. This is especially true for the *Coprinaceae*, those with strong autodeliquescent properties, as well as those without them. In the species with tough carpophores, some thickwalled basidia are occasionally found, and even in soft species such as *Armillariella mucida*, occasional basidia with thick walls and a generally sclerotized appearance can be observed. Even if they have distinct

[1] In a paper published after this manuscript was edited, June 1948) *Studies in the basidium*, E. J. H. Corner points out that, disregarding a few exceptions the volume of the basidia minus that of the initial vacuole equals the volume of the spore multiplied with the number of the spores per basidium.

sterigmata, they always appear empty, and it may be suspected that a cytological investigation of this problem will show them to be pseudoparaphyses (see p. 104). Only one species and genus known at present has typically thick walled basidia of normal function: *Phaeomycena albidula*.

The order or sequence of maturation of the basidia in the hymenium has been studied by Buller. However, in taxonomy it is not yet accepted usage to rely on more than the two main types of hymenophores named by Buller, viz.

1. *The inaequihymeniiferous type of hymenophore (or carpophore).* Buller who is not the first to have observed this type, is, however, the one who has most thoroughly studied the subject and coined the terms, and therefore his terminology is here accepted (Buller, 1922). In the inaequihymeniiferous type, the hymenophore consists of lamellae which are parallel sided or almost so, rather thin (trama of small diameter), and they are brought into approximately vertical positions through a negatively geotropic stimulus in the growth of the stipe; the lamellae themselves are not always completely vertical, and one side of the lamella may be turned upward while the other side is turned obliquely downward; the hymenium develops unequally on different parts of the lamellae, generally starting to mature at the edge and continuing slowly upwards along the sides of the lamellae; each small area (0.1 mm²) does not produce a number of successive generations of spores, but all the basidia on the area mature almost simultaneously. The spores are discharged in succession from below upward, and a zone of autodeliquescence follows, destroying completely those parts of the lamellae where the spores have been discharged (Pl. XII, 1; XX, 3).

2. *The aequihymeniiferous type of hymenophore (or carpophore).* Buller distinguishes this type from the above by the shape of the hymenophore, the development of the hymenium and the manner of discharge of the spores. The hymenophore is lamellate and consists of « gills which are shaped like the blade of a pen knife ». The thickest part of each lamella is attached to the context of the pileus whereas the more or less sharp edge is turned downward; the sides of lamellae are therefore not parallel; a cross section of the lamellae is wedge-shaped. The lamellae are positively geotropic during their development, and their median planes are brought into vertical positions, even if the stipe should not be vertical and straight; the younger the lamellae, and the less the angle of tilt, the greater is the

success which the lamellae attain in bringing their median planes back into vertical position once this has been altered; consequently, the normal lamella has both sides facing outward and slightly downwards at the same angle. The hymenium, in each small area, develops equally, i. e. the basidia do not mature in zones starting from the edge upwards, and the production of basidia takes place in succession. During the spore discharge, the hymenophore is not deliquescent.

Buller has not studied the corresponding types in the boletes, but he has subdivided each of his types into a whole series of subtypes which, at present, are not used in taxonomy. This, however, does not mean that a more complete study of the species belonging to each subtype will never furnish any additional taxonomic characters for the distinction of sections, or perhaps even genera. The most important use of this character was made when the generic position of *Pseudocoprinus disseminatus* was investigated (see under that genus).

The immature basidia, often (perhaps incorrectly) called basidioles) [14], are usually of approximately the same shape as the mature basidia, only often slightly to considerably smaller, or narrower, or rather more fusiform than clavate. Fusiform basidioles are rather characteristic for certain genera, such as *Marasmius*, *Marasmiellus*, and *Collybia*, also certain smaller tricholomataceous genera, related to these three (Pl. XXVIII, 2, *d-e*).

In most species of the inaequihymeniiferous type and in but a very few of the aequihymeniiferous type of agarics, the basidia are separated by and dispersed in a more or less regular manner, among pseudoparaphyses (see p. 104). Or, as Buller describes this situation

[14] Boudier and Romagnesi use this term for what we call pseudoparaphyses, or aborted basidia, and Petrak uses the word pseudoparaphyses for a certain type of paraphysoids in the *Ascomycetes*. We use the word basidioles in the sense in which it is used by most cytologists and taxonomists in the *Agaricales*, i. e. as term for the young binucleate basidium with meiosis; the following stage during the nuclear divisions has been called metabasidium by Donk but this term is also used in a somewhat different sense in other groups of fungi. The word pseudoparaphyses is here used exclusively for the consistently sterile, often slightly modified, non protoplasmatic basidia, since in the *Myrangiales* the term paraphysoids (remainders of the interthecial stroma) is sufficient and satisfactory. — Heim attempts to apply the term basidioles to both young basidia and pseudoparaphyses « they constitute basidia which are young or arrested in their development ».

for the inaequihymeniiferous type and the *Psathyrella* subtype of the aequihymeniiferous type, pseudoparaphyses « are normal constituents of the hymenium. They are very large and are united so as to form a pavement through which the basidia protrude. They not only support the basidia mechanically but act as space-makers so that adjacent basidia are separated from one another by a distance just sufficient to prevent any jostling during spore development and spore discharge » (3 : 122, 1924). This arrangement of the basidia is paralleled by a definite dimorphism, more rarely a trimorphism, or tetramorphism of the basidia, expressed in the distance by which they project above the pseudoparaphyses, their shape and the time at which they develop — the least projecting basidia being the ones that belong to the latest generation. All these characters are included when a hymenial structure is called coprinoid. The coprinoid hymenial structure (Pl. XII, 1) is among the characters that distinguish *Xerocoprinus* from *Coprinus*, and *Pseudocoprinus* from *Psathyrella*.

Of all these characters, Fries concentrated his attention on the only one that is macroscopically visible, viz. the autodeliquescence. However, the autodeliquescence is not understandable unless the shape of the lamellae in *Coprinus* is taken into consideration. The equal diameter of the hymenophoral trama makes spore dissemination difficult. In those species that have angiocarpous development and toughish consistence, the problem is solved by postponement. In the ephemerous species with agaricoid, i. e. non-angiocarpous development, and fragile consistency, the problem can be solved in two ways, either by transformation of the lamellae into wedge-shaped formations — or by autodeliquescence, i. e. by removing the lower part of the lamella that would hinder the free fall of the discharged spores, from the zone immediately above. At the same time, the spores that have accidentally stuck to the hymenium or have not come clear from it, are suspended in a fluid that drops onto the grass, or is taken off by passing animals, hereby receiving a second chance of dissemination. Both the wedge-shaped lamella and the autodeliquescent lamella are realized in the family *Coprinaceae*. Since animals play a certain rôle in the explanation of the latter type of spore dissemination, it is not surprising that the truly inaequihymeniiferous *Coprini* are often found on animal excrements, such as horse manure, rabbit-, deer-, and cow dung, etc., and also on manured fields, white-mushroom beds, and manure heaps.

Cystidia

The word cystidia (cystides, Léveillé, 1837) in its broadest sense designates any sterile bodies that are interspersed in the hymenium or replace the basidia in any part of the hymenophore, or — according to later emendations of the term — occur on one of the usually sterile surfaces of the carpophore but resemble the hymenophoral cystidia which are apparently homologous with them. However, this traditional definition of the cystidia, has recently been — step by step — abandoned in favor of narrower terms. Since the presence or absence of cystidia in the broader sense is not always a constant character, a differentiation between the various types of cystidia is desirable from a taxonomic point of view as well as from a purely morphological, anatomical, and physiological viewpoint.

The main classification of these sterile bodies in the concepts of some authors derives from the distribution of the cystidia on the carpophore. Some authors use the following terminology which we think is rather superficial and not truly morphological though its simplicity has much to recommend it. For this reason we mention it here. It divides the cystidia into the following categories: Cystidia A. on the hymenophore (a) on the sides of the lamellae or the interior of the pores: *Pleurocystidia*. — (b) on the edge of the lamellae or pores: *Cheilocystidia*. — B. on the sterile surfaces of pileus or stipe (a) on the pileus *Pilocystidia*. — (b) on the stipe *Caulocystidia*.

This scheme calls pilocystidia the cystidia like bodies on the epicutis of the pileus in *Russula emetica*. If exactly the same type and subtype of bodies occurs on the stipe of *Russula emetica*, it is called caulocystidia. However, entirely different cystidia like bodies occurring on the pileus of *Flammulina velutipes* are given the same name as those occuring on the pileus of the *Russula*; and the elements of cystidia-like appearance found on the stipe of *Leccinum scabrum*, though quite different in shape, chemical characters, and origin from those of the *Russula*, are called caulocystidia in the *Leccinum* as well as in the *Russula*. Actually, the pilo- and caulocystidia of the *Russulae* are homologous and practically identical whereas the pilocystidia of *Flammulina* and the caulocystidia of *Leccinum* belong to very different types.

Those cystidia like bodies that are found in the hymenophore, on the edge as well as the sides of the lamellae of many *Russulae* and

Lactarii should be put in a category by themselves because of their origin in (or homology with) the conducting system of these genera. By their very nature, they are merely prolongations of the conducting system into the hymenium, or into the epicutis of the pileus or the covering layer of the stipe. This kind of cystidia has been called pseudocystidia by Kühner and Romagnesi. They were first recognized as «false cystidia» («simulant des cystides», by Boudier (1866). We apply the term pseudocystidia as a general name for all cystidia derived from conducting elements, whether they otherwise belong to the laticiferous system, or oleiferous hyphae, or the gloeo system, or the coscinoids.

Pseudocystidia are common in the *Russulaceae*, in *Lactocollybia*, in *Lentinellus*, and *Linderomyces*. In each of these cases, however, the type of pseudocystidia occurring is different, and has received different names. The subtype found in the *Russulaceae* and *Lentinellus* is known as macrocystidia (Romagnesi, 1944). It is characterized by a chemical feature, viz. the discoloration with acid aldehyde solutions, and the weak absorption of cresyl blue by its contents. Another subtype has for a long time been known as gloeocystidia; however, the existence of gloeocystidia in *Agaricales* was not known until recently. It is found in *Russula polyphylla* and probably also in some other species of the *Russulaceae*, in *Lactocollybia* (Pl. XXI, 3), etc. The gloeocystidia can be recognized by the oily contents that are often very distinct but sometimes absent, and, more clearly, by the deep blue color they assume when stained with cresyl blue (excepting the walls which remain a pale violet color). This metachromatism is, on the basis of what is known at present, an infallible sign that the bodies showing it are part of the gloeo system or, more precisely, gloeocystidia. The third subtype is rare, and it is called coscinocystidia because of the sieve like character of their surface. They are protruding cystidia like ends of the coscinoids and have been observed only in *Linderomyces*.

The remaining subtypes of pseudocystidia have not been named separately, and are characterized by three negative characters (1) by not darkening with acid aldehydes (2) by not having completely deep blue contents when dyed with brilliant cresyl blue (3) by having an entire rather than a sieve like surface. These subtypes of pseudocystidia should at present be referred to in a general way, as pseudocystidia or pseudocystidial stages of certain other types of cystidia.

All organs that answer the general description of cystidia in the

wider sense but do not fall into the category of pseudocystidia, are true cystidia.

Not all true cystidia have their origin in the deeper layers of the subhymenium, or in the trama. Some originate at exactly the same level as the basidia, and differ from the basidia and pseudoparaphyses merely in shape. These are called cystidioles. True cystidioles are frequently found on the sides of the lamellae (Pl. XX, 3; XXI, 4; XXVIII, 2 *f*) or in the interior of the tubes, and in certain groups they are rather characteristic. If they occur on the edge of the lamellae and lamellulae, excepting the attenuate portion of the latter, or the pores exclusively, they should be referred to as cheilocystidia (Buller, 1924). We cannot believe it necessary or advantageous to differentiate between the cheilocystidia that are, according to the position of their mothercell, localized cystidioles, and those that derive directly from the trama because of the lack of a subhymenial layer at the very edge as is often observed in *Collybia* [13] (Pl. XIX, 4; XXV, 2; XXIII B, 1, 3-4, 6; XXVIII, 2 c, g).

Another category of true cystidia has its origin in the tramal hyphae, or, in some cases in the lower part of the subhymenium, at a deeper level than the basidia. Except for their deeper origin they do not essentially differ from the cystidioles in their development or in their resemblance to the basidia. The cystidia of many boletes come into this category (Pl. XIX, 3), and since it appears that Romagnesi's term leptocystidia (1944) belongs here, we shall accept it. However, the leptocystidia sometimes have a tendency to be rather firm and have partly thickened walls (*Gomphidius viscidus*; Pl. XXVII, 7), or even thickened and colored walls, in which case we call them setuloid cystidia, or for short « setae » [14] (Pl. XV, 2-3).

In certain genera, all transitions between cystidioles and leptocystidia can be found in a single section.

[13] The cheilocystidia of *Collybia peronata* and related species are also remarkable for their development which seems to be retarded; they are much more inconspicuous and scattered in young specimens than in mature carpophores.

[14] Setae of the type observed in the *Aphyllophorales* such as *Phellinus* and *Hymenochaete* are in the opinion of some authors, not observed in the *Agaricales*; however, it is customary to call setae the organs found in *Boletochaete*, *Marasmius cohaerens*, etc. But they are not always colored even in the same hymenium, and are variable in color (fulvous, rufous, chestnut, green), in *Chaetocalathus*, the setae-like bodies are hyaline and become deep brown only after they have been treated with iodine solutions.

Anybody who studies the relationships between the morphology of a given organ and its function will not be surprised to find that the terminology indicated above meets certain difficulties when more single cases, and their different stages of development are analysed. The most intriguing problem is that of the deep rooted cystidia of the type found in *Panus rudis* and related species, *Pleurotus floridanus*, and perhaps some related Asiatic species, and in all the species of the genus *Hohenbuehelia* (Pl. XXII, 2), also in all cystidiate *Inocybae* (Pl. XVII, 1). Donk has shown (in an unpublished manuscript that the author had the privilege to see) that the same type of cystidia is also found in *Peniophora*, and is called metuloids by Cooke (1879). These bodies start out by being pseudocystidia in the sense that they appear to be proliferations of the conducting system into the hymenium (yet, neither belonging to the subtype of the macrocystidia, nor the gloeocystidia, nor the coscinocystidia), and serving as excretive organs. Later on, they become thick-walled, loose their excretive function, and strongly resemble the leptocystidia, were it not for the fact that they are uniformly deep rooted, uniformly thick-walled, and mostly hyaline to straw colored and always non-amyloid. Deposits of coarse crystals are often found even on the old metuloids, especially at the apex, but sometimes all over. This kind of cystidium has often been called «*Peniophora* cystidium» by mycologists (including this author) but the term metuloids appears to have priority, brevity, precision, and descriptiveness in its favor. Romagnesi (1944) calls them «lamprocystides».

In certain cases, we find that typical macrocystidia, or gloeocystidia, originate not from portions of the conducting system, but become part of it at the very septum that separates them from the next lower hypha, or in certain cases, they become, theoretically speaking, part of the conducting system from a certain level inside themselves, e. gr. many of the macrocystidia of *Russula nauseosa*. Typical of this kind of pseudocystidia is also the cystidium of *Pholiota astragalina*, *Stropharia aeruginosa*, *Naematoloma fasciculare*, and allied species. Few of these cystidia are continued into anything that might be called portions of the conducting system, yet, chemically, they are pseudocystidia. In certain individual cases, they are really cystidioles, or leptocystidia from an anatomical point of view, but the strong absorption of cresyl blue by their contents reveals them to be part of the conducting system even though they may not be directly connected with its internal portion but instead represent a transmu-

tation of ordinary structural hyphae into pseudocystidia at the level where they enter the subhymenium or the hymenium. Romagnesi (1944) has called this type chrysocystidia (Pl. XVII, 3) because of the internal body that is typically colored yellow when ammonia is used as a mounting medium [15]. This term, in the author's opinion, is worthy of being taken up in descriptive mycology, just as well as the term metuloids.

There is nothing unusual in considering macrocystidia as well as the chrysocystidia to be pseudocystidia even if they arise from an ordinary hypha. It can be noticed in most sections of the cortical layer and the context immediately underneath in a large number of agarics, that normal hyphae (of the fundamental system) often, at a certain point, become oleiferous; this is especially true of the so-called « laticiferous hyphae » of *Russula*, which turn deep blue in sulfovanilline; this reaction makes it possible to observe this sudden transition with ease.

It is therefore obvious that an absolutely sharp line between pseudocystidia and true cystidia cannot be drawn because (1) in some cases, the origin of otherwise typical pseudocystidia may be hyphal rather than « vascular »; (2) in other cases, the development of the individual pseudocystidium may include both a pseudocystidial and a cystidial phase.

There are still cases that are not fully investigated chemically, and the function of the cystidia as well as the origin remains unknown. It is a wise policy, in all these cases, to refrain from using any of the above terms, and merely refer to cystidia (in the widest sense).

Only the cystidioles can, from a morphological point of view, be considered as transformed basidia, i. e. basidioles (young basidia) that because of a change in function [16] or by loss of their function as gonotoconts do not turn into normal spore bearing basidia (Pl. XXVIII, 2 *a*) but rather assume an often characteristic, more or less constant shape in accordance with their function and cytological development.

[15] This internal body can also be stained with ferric acetocarmin as used for the *Lyophyllum*-basidia (see below, p. 103)

[16] In *Coprinus*, the cystidioles have assumed a mechanical function, probably holding the lamellae in equal distance; in *Melanoleuca*, the cystidioles seem to have an excretive function as evidenced by the crystal hood; in *Tylopilus plumbeoviolaceus* and in *Gymnopilus cacaophyllus*, the basidia of young hymenophores are so strongly incrusted with a fulvous resinous matter that they are often retarded or transformed into pseudoparaphyses.

However, even this very differentiation in shape is frequently indicative of their basidial origin. Some of the cystidioles still go through the motion of forming sterigmatoid prongs, but the latter are more irregular in number and shape, often limited to one. In a few cases, the cystidioles even develop an homologon of the spore on the sterigmatoid prong (called mucro) which is then capitate with a stalked, well-delimited capitellum. In extreme cases, the mucro or the capitellum is easily detached from the cystidioles and floats around in preparations of the hymenium. This capitate type of cystidiole is found in the cheilocystidia of *Conocybe* (Pl. XIX, 4) and *Pholiotina septentrionalis*. A good example of transitions between basidia and cystidioles is found in *Omphalotus olearius*.

The term paraphyses, often found in the literature on Basidiomycetes, even in the sense of cystidia, but more commonly to designate the pseudoparaphyses of Kühner and the «basidial cells» of Corda, should be discarded in this class of fungi (see p. 39, foot note 14).

Since the distribution of the cystidia is often different on the edge of the lamellae and pores or contrasted to the sides of the lamellae and interior of the tubes, Maire has proposed to call the edges

1. *Heteromorphous*, if they are sterile (or predominantly so, because of the presence there of a type of cystidium (cystidiole) that does not occur on the sides of the lamellae (or in the interior of the tubes). We may logically designate as inversely heteromorphous the opposite case where the edge alone is completely free of cystidia.

2. *Subheteromorphous*, if the edges are sterile (or predominantly so) because of the density of the same type of cystidia that is scattered among the basidia on the sides of the lamellae (or the interior of the tubes).

3. *Homomorphous*, the hymenium on the edges is not differentiated from that on the sides.

Romagnesi (1944) has suggested the term «pseudoheteromorphous» for those cases of heteromorphism where the cystidia occur only on the edge without being homologous with any dermatocystidia («hairs»), as is the case in *Psathyrella Candolleana*. The term «pseudoheteromorphous» is based on the somewhat precarious differentiation of two types of what is here called cheilocystidia, viz. those cheilocystidia that are comparable with the «hairs» of the cortical layers (of pileus and stipe) rather than with hymenial cystidia, and those that are not. The fact that the hymenium is, in many primordial and young stages of agarics and boletes extended beyond

the hymenophore proper, makes it very difficult to justify this differentiation on a morphological basis.

Since a variable number of fertile basidia is often found in an otherwise heteromorphous or subheteromorphous edge, it is necessary, in these cases, to refer to « almost heteromorphous » and « almost subheteromorphous » edges.

XI. THE STERILE TISSUE OF THE HYMENOPHORE

The hymenium is only a thin outer layer of an organ usually referred to as hymenophore, i. e. a part of the carpophore, modified and especially adapted to provide a maximum of surface space for the hymenium.

In only a few *Agaricales* the hymenophore is wanting. It is then replaced by a smooth hymenial surface, the basidia either originating from a subhymenial layer or directly from the lower or upper surface of the trama of the pileus or cup or whatever the hymenophorous part of the carpophore may be. This smooth hymenial surface may be a first stage in the development of the carpophore or, in other cases, it may be a permanent reduction of more or less constant occurrence, or, again it may be a primitive form of development. These heterogeneous groups of genera, that have in the past been assembled in the *Thelephoraceae*, partly belong in this last category. In the *Agaricales*, we find this character exceptionally rather than constantly, except for a few genera that may well be interpreted as strongly reduced forms (some « *Cyphellae* », *Physalacria*). In others, we find mature hymenia of the same species, sometimes smooth, sometimes covering a lamellate hymenophore, or a venose hymenonophore (*Marasmiellus*, *Marasmius*, *Mycena*, *Delicatula*). It must now be assumed that some species that where initially described as or considered as *Helotium*, or *Cantharellus* are actually *Agaricales* with either smooth, or venose hymenial surface. However, the so-called veins of such species as *Cantharellula umbonata* (*Cantharellus umbonatus*) or *Hygrophoropsis aurantiaca* (*Cantharellus aurantiacus*) are not true veins of the type encountered in *Cantharellus cibarius* but rather lamellae with more obtuse edges.

In all but the exceptional cases mentioned above, and perhaps in *Geopetalum carbonarium* (A&S ex Fr.) Pat., the hymenophore of the *Agaricales* has either the shape of lamellae or of tubes. The examin-

ation of the internal structure of the hymenophore in these forms, i. e. the anatomy of the hymenophore minus the hymenium, is of great importance in taxonomy. The internal structure of the lamellae and tube walls is studied on longitudinal sections from the plane of attachment to the trama of the pileus down to the edge of the lamellae or the pore edges. In lamellate as well as in tubulose forms, care must be taken to cut exactly at a right angle to the edge of the lamellae [19], and exactly in the direction of the individual tubes rather than obliquely, i. e. in all cases, the section must be exactly vertical; it must also be exactly tangential, i. e. the lamellae should be sectioned at a right angle to their sides. It is also important that these sections are reasonably thin (about 15-20 μ) because otherwise pressure on the cover glass has to be exercised in order to obtain a preparation transparent enough to show the arrangement of the single elements of the trama and adjacent layers. However, there is always a slight disorganization in such preparations, and if they are taken from old or otherwise poor material, the results will be unreliable. Under no circumstances may the preparations be crushed to the point where its elements are so dislocated that it is impossible to make an analysis of their arrangement. The beginner, and those who have to handle material that is very scanty, brittle, or otherwise difficult to handle, and also those who find it difficult to learn sectioning by hand in the manner described above, are strongly advised to use a microtome. Both freezing and paraffin methods will do.

It appears that the sterile internal portion of the hymenophore consists of one or several layers. If there is only one, it is called the hymenophoral trama, or for short the trama [20]. But more frequently

[19] In ascendant lamellae the hyphae often do not run to the edge at a right angle, and in this case the section should be oblique in the sense of the direction of the hyphae as otherwise their true proportions may be misinterpreted.

[20] Some authors use the word trama exclusively for the trama of the hymenophore. There is, however, no reason to reserve the term for only a single organ since the trama is not sharply delimited at the plain of attachment of the hymenophore to the pileus in the majority of the species. Only very rarely is there a differentiation between these layers (hymenophoral trama gelatinous, trama of the pileus nongelatinous in *Dictyopanus pusillus*), and even then, the trama of the hymenophore originates in the trama of the pileus. It is therefore more precise and generally preferable to specify as to the part of the trama considered, viz. the hymenophoral trama, etc. If the word trama is used alone, it should either be quite clear from the text or the arrangement that the hymenophoral trama is meant and none other, or else it must be supposed that whatever is said about the trama refers to all parts of the trama in the widest sense.

there are two or more equal layers on both sides of the central hymenophoral trama, more or less easily discernable between the hymenophoral trama and the hymenium proper. If there is only one such layer, it is referred to as subhymenium, always consisting of small elements with numerous septa. If there is another layer between this and the hymenophoral trama, distinguishable from both the former and the latter in structure or characters of the elements composing it, it is called hymenopodium.

The hymenophoral trama occurs in four main types of structure:

1. intermixed to irregular (Pl. XIX, 5; XXI, 1, 5)
1. subregular to regular (Pl. XXII, 3)
3. bilateral (Pl. XXII, 1)
4. inverse (Pl. XX, 2)

The difference between intermixed and irregular trama is secondary; both are characterized by completely or at least predominantly irregular arrangement of the hyphae which are neither parallel (not even approximately so) nor divergent. In the subregular trama and the regular trama, the hyphae run approximately or strictly parallel (approximately in subregular, strictly parallel in the regular trama), i. e. from the plane of attachment to the pileus down to the edges. In the bilateral trama, there is a central strand which is subregular or regular as described above but much thinner in diameter, and an outer layer consisting of approximately parallel hyphae but which are not straight or parallel with the hyphae of the thin central strand but curve outward on both sides, joining the hymenopodium, or subhymenium, at a point farther outwards toward the edge of the pores or lamellae than the point at which each individual hypha departed from the thin central strand. The thin central strand is called the mediostratum, and the divergent portion of the trama on both sides is called lateral stratum. The nature of the hyphae involved may be rather different. Sometimes, the hyphae of the mediostratum and the lateral stratum are of approximately the same type; but in other cases, the average diameter may be different in the hyphae of the mediostratum and the lateral stratum; the pigmentation may also be different, and the gelatinization, and consequently the density, the frequency of septation, etc. may differ in those two layers. Although it is true that it is mostly the hyphae of the fundamental tissue that are primarily responsible for the structure of the hymenophoral trama, in some cases, it appears that at least the more conspicuous part of the elements composing the trama and marking

its arrangement is made up by the conducting elements; e. gr. in *Linderomyces*, where the consciroids diverge, almost without forming a distinct mediostratum, soon assuming a position perpendicular to the sides of the lamellae, thus making the hymenophoral trama very strongly (yet not quite typically) bilateral. There are also various types of bilaterality insofar as the relative density and diameter of the hyphae are concerned. The bilateral hymenophoral trama of *Catathelasma* consists of very thin hyphal elements whereas that of *Amanita* consists of rather broad and moderately long elements.

If the elements composing the hymenophoral trama differ from each other fundamentally, showing two main types of elements, thin, elongate, hyphal elements and swollen, voluminous, subisodiametric elements (« sphaerocysts »), the trama will logically be neither subregular nor regular; it will also not be bilateral unless the juxtaposition of these two types would coincide with what may be called a mediostratum and a lateral stratum. It is obviously a special case of an irregular trama, and it is called intermixed trama, i. e. a trama where two types of elements are « mixed » with each other.

If the hymenophoral trama consists of a mediostratum and a lateral stratum, the latter consisting of hyphae curving outwards but reaching the subhymenium farther away from the gill edge rather than nearer to it as in the bilateral trama, we may assume with Fayod (who discovered this strange structure) that here the origin of the hymenophoral trama is in the subhymenium rather than vice versa. Perhaps, the isolated manner of development of the fundamental hyphae (here the hyphae of the lateral stratum), often observed in the trama of the carpophores of the *Amanitaceae*, manifests itself in the species with the kind of hymenophoral trama described above in that each subhymenial hyphal ramification produces either a hymenial element (on the outside), or an element of the fundamental tissue, more precisely the lateral stratum (on the inside). Further investigations must show what the origin of the mediostratum is. Whatever its morphological and ontogenetical significance, this type of hymenophoral trama is of as great taxonomic importance as the other types, and has been named inverse trama (trama renverse, Fayod, 1889). Good examples for intermixed trama are the *Russulae*; for irregular trama — *Pleurotus*; for subregular trama — *Hygrocybe* excepting the section *Conicae*; for regular trama — *Hygrocybe*, section *Conicae*; for bilateral trama among the boletes — *Boletus edulis* and all the other *Strobilomycetaceae* and *Boletaceae*, among the agarics -

Amanita caesarea and all the other species of *Amanita*; inverse trama — *Pluteus* (all species known), and related genera.

Less important differences in the structure of the hymenophoral trama can be distinguished as subtypes of the above basic types. These are:

1. *The* Phylloporus *subtype of the bilateral type:* The lateral stratum is scarcely looser than the mediostratum, hardly less colored, and only slightly more gelatinized, only slightly more divergent, and with the hyphae usually touching each other. Example: *Phylloporus rhodoxanthus* and most species of *Xerocomus*.

2. *The Boletus subtype (« truly bilateral »)*: The lateral stratum consists of hyphae that are less colored than the mediostratum, distinctly removed from each other (because of stronger gelatinization), and at first strongly curved. Example: *Boletus edulis*, and most other boletes.

3. *The subbilateral subregular subtype of the regular type*: The outermost hyphae of the otherwise regular hymenophoral trama show a very slight tendency to diverge but a mediostratum is not differentiated. Example: *Clitocybe dealbata*.

4. *The regular subcellular subtype of the regular type:* The elements of the otherwise regular trama are so grossly enlarged and broadened that the trama appears almost cellular at places. Example: *Mycena*, *Psathyrella*, *Pseudocoprinus*.

In certain genera of the *Tricholomataceae* (many *Resupinateae*, *Dictyopani*, etc.) and in some *Crepidoti*, the trama is partly or entirely more or less gelatinized. In *Panus*, *Pleurotus*, also in some species of *Marasmiellus*, in *Heimiomyces*, *Anthracophyllus*, etc., the trama consists mainly of thick-walled, rather large, rigid, elongate hyphae, and in this type of trama, the thin walled, thin, small, curved elements of the connective tissue are naturally more conspicuously different from the other elements which belong to the fundamental tissue. This difference may be expressed in calling this type of trama intermixed rather than irregular or subirregular, but it is obvious that this meaning of « intermixed » is not identical with what it is in *Russula*.

In a few cases where the trama proper is strongly reduced in favor of a hymenopodium (rarely a subhymenium), the impression may prevail that the hymenophoral trama itself consists of two layers with the lateral stratum running exactly parallel with the mediostratum instead of diverging. This is the case in *Conocybe* (Pl. XXI, 2). In this

case we may speak of false bilaterality. In *Gomphidius*, especially *Chroogomphus*, the hymenophoral trama is basically bilateral, yet, the divergence of the lateral stratum is obscure by an increasing irregularity of structure as the carpophores mature while the mediostratum is so reduced it is hardly recognizable especially in old specimens. It is consequently easy to mistake the broad hymenopodium that is not sharply delimited from the subhymenium, either for the lateral stratum of the hymenophoral trama, or for an unusually enlarged subhymenium.

This strong development of the hymenopodium is noticeable only in a small minority of the *Agaricales*. The hymenopodium is completely irregular in those *Agaricales* with lamellate hymenophore but otherwise related to the boletes (*Gomphidiaceae*, *Paxillaceae*), and it is regular and consisting of broad, voluminous hyphae in *Conocybe*. It is also somewhat developed in some species of *Russula*, *Mycena*, etc., where, however, its taxonomic significance, as far as can be seen now, never goes beyond the species level.

The subhymenium is rather uniform. It is rarely of great taxonomic importance with the exception of the genus *Pleurotus* (Pl. XXI, 1 where it is well developed in contrast to *Panus* (Pl. XXI, 5) where it is almost absent, and *Leucopaxillus* where it is filamentous (ramose), whereas in *Armillaria* it is cellular. This latter difference is not always so sharp as in the case of *Armillaria* and *Leucopaxillus*. This can be seen in some species of *Gomphidius* where the crowded septa shorten the individual cells so much that the whole seems to be a minutely pseudoparenchymatic tissue. Wherever the septa are not so close, the subhymenium assumes a more filamentous character. Wherever the elements become irregular in shape and denser and more intricately interwoven, we have an intermixed subhymenium, as is the case in *Gomphidius*, subgenus *Chroogomphus*, or *Omphalina*, subgenus *Romagnesia*, or some species of *Resupinatus*.

In these species of *Resupinatus*, the trama proper of the lamellae is gelatinized, looser and more regular. In other groups, especially the section *Lactae* of the genus *Hygrocybe*, the hymenophoral trama is non gelatinized while the subhymenium is strongly gelatinized. This is one of the very few cases where the large diameter and strong differentiation of the subhymenium may lead to the misinterpretation as though the trama proper were bilateral whereas, actually, here again, we have an example of false bilaterality.

In genera with regular trama, the subhymenium is often separable

from the hymenophoral trama, and then lamellae are macroscopically described as fissile, a feature frequently found in agarics but hardly of much taxonomic value.

The subhymenium usually accompanies the hymenium all through the interlamellar zones at the top of the interlamellar space, and in certain cases, the hymenophoral trama or its parts run parallel with it. In this case, a looser layer of differently organized hyphae separates the hymenophore from the trama of the pileus. As a consequence, the hymenophore can be easily separated from the context of the pileus. This is especially remarkable in *Paxillus*, and most *Boletaceae* and *Strobilomycetaceae* where the hymenophoral trama is bilateral and forks above the level of attachment of the hymenophore to the trama of the pileus — thus facilitating the separation of the tube walls or lamella together with the ceiling of the tubes or the interlamellar zones.

Certain agarics possess a special epiphyllous zone of a structure different from that of the trama of the pileus as well as the trama of the hymenophore. This may also result in an increased separability of the hymenophore as a whole.

The structure of the hymenophoral trama has at present become one of the most important characters in the *Agaricales*. Tribes, genera, even families are based on the structure of the hymenophoral trama wherever this character is correlated with other important features. There can now be no methodical analysis of any representative of the *Agaricales* without a careful study of this particular character.

XII. CORTICAL LAYERS

Cortical layers are formed by a differentiated tissue forming the surface layer of the pileus and stipe of the *Agaricales*. We have already seen (p. 41) that cystidioid bodies, reminiscent of those that occur in the hymenium either on the sides of the lamellae or in the interior of the tubes — or on the pore or lamella edges, are also found in the cortical layers as relics of an originally indiscriminately expanded hymenium, or as products of a further differentiation of the cortical layers whereby they may have assumed some specific function. The cases where these cystidia are remainders of a primordial hymenium are not rare in the *Boletaceae* and *Strobilomycetaceae*, e. gr. *Suillus*, sect. *Granulati* (Pl. XXV, 8 9); the reticulate *Boleti*, and

Tylopili, all species of *Leccinum* (Pl. XVI, 5), and the alveolate species of *Porphyrellus* and *Boletellus*. Here, the ornamentation of the stipe is still reminiscent of the configuration of the hymenophore. In many of these, even sporulating basidia are found among sterile bodies making up the palisade of the cortical layer covering these ornamentations, especially in the upper portion of the stipe. In rare cases even the whole marginal zone of the pileus is covered by a hymenium, a large portion of which consists of basidia (Pl. XXVI, 5). All this is proof enough that these bodies are of hymenial origin. It is very difficult to state in every single case, whether the elements of the cortical layers are of hymenial origin, or later acquisitions due to an increasing differentiation and division of functions. It is not even certain that, if these elements should have been differentiated in a later stage of the evolutionary development of a genus, they cannot have originated from the hymenium or an extension of it. In such cases as *Russula Mariae* where we find the same type of elements on the edge of the lamellae and on the cortical layers, it may well be that they are both modifications of a degenerated hymenial element.

Considering all this, it does not seem possible at present to distinguish between such cystidioid bodies that have a non-hymenial origin and such that evidently originate from hymenial elements. Consequently, it is, in the author's opinion, correct to refer to all cystidioid bodies of the cortical layer as cystidia or pseudocystidia, if they are in some way comparable with either cystidia or pseudocystidia of the hymenophoral hymenium, with the only difference that those bodies that occur in the cortical layers receive the prefix dermato-. Thus, we have, in the cortical layers:

1. dermatocystidia (Pl. XXV, 9); 2. dermatopseudocystidia (Pl. XV, 1).

Although it is not customary to refer to «dermatogloeocystidia» or «dermatocystidioles» or «dermatometuloids» or «dermatochrysocystidia» or «dermatomacrocystidia», etc. (all these bodies are being called dermatopseudocystidia or dermatocystidia), it is correct to call the basidia occurring on the stipe or the pileus, outside the area covered by the hymenophoral formations, dermatobasidia, and those of them that remain permanently sterile with slight modifi-

[31] Naturally, with a subhymenium in the proper sense being absent in the cortical layers, it would be difficult to state whether a dermatocystidium has cystidiole character or not.

cations in size or shape, but strongly differ from the cystidia, — as dermatopseudoparaphyses.

Dermatobasidia are found on the pileus of *Boletus subsolitarius* and many *Russulae*, and much more commonly on the apices of the stipes of the boletes and agarics. If fertile dermatobasidia occur in a hymenium-like structure on the surface of the pileus or the stipe, we may then refer to that structure as to an extension of the hymenophoral hymenium, and call it extrahymenophoral hymenium. If there is a hymenium like structure outside the hymenophore that lacks dermatobasidia and, for that matter, also dermatopseudoparaphyses, we call this structure — hymeniform, and the layer, made up by it, a hymeniform layer (Pl. XIII, 2).

If the cortical layer is formed by hair like septate hyphae, i. e. hyphae inserted more or less perpendicularly to the surface of the organ in question yet not being strictly hymeniform, it is called trichodermium (Lohwag, 1937, 1941; Pl XVII, 3; XXVI, 1); if the trichodermium is gelatinized as in *Suillus granulatus*, it is an ixotrichodermium (Snell, in Elrod & Blanchard, 1939). These hyphae usually form a velutinous to tomentose surface, but at times, especially when densely interwoven, they are not easily recognizable macroscopically; in the ixotrichoderma, the surfaces covered by it are, as a rule, merely glutinous. If the hyphae are vertical (erect) and parallel with each other, we speak of a trichodermial palisade (Lohwag, 1937, 1941) which differs from the hymeniform layer in that not necessarily every element originates and ends at the same level as the neighboring elements of the same nature [11]. Trichodermial palisades (Pl. XVIII, 1; XX, 1; XXV, 1; XXVI, 2 4) usually make the surfaces they cover velutinous, or granulose, or pruinose; they never show a watery, smooth surface, nor are they coarsely tomentose. The rimose or rimulose surface (as in contrast with the rivulose surface) in many boletes is a result of this kind of structure, that easily lends itself to perpendicular cracks that spread tangentially in all directions. Trichodermial palisades are also common in the *Agaricaceae*. The terminal members of the hyphae forming trichodermial palisades frequently are cystidioid, i. e. they are dermatocystidia, probably in most cases of the leptocystidia- and cystidiole type (example: *Phaeomarasmius*).

If the trichodermium, especially the trichodermial palisade, con-

[11] According to these definitions, the hymeniform layer is a special case of a trichodermial palisade.

sists of shortened hyphal elements that tend to become sphaerocysts (isodiametric hyphae), the result is a mass of subglobose or globose bodies — with or without showing the original catenulate arrangement — that can be characterized as a loose pseudoparenchymatic layer. This type of cortical layer is called epithelium (Lohwag, 1937, 1941), or a cellular layer (Pl. XVII, 4; XXVI, 7). If there is only one stratum of sphaerocysts which are, with their base, directly attached to the hyphae of a lower layer, it is often difficult to differentiate between a hymeniform layer and an epithelium inasmuch as some of the sphaerocysts of the epithelium are often mucronate at the distal end or slightly vertically elongated (short ellipsoid or short clavate). The pluristratous epithelium is closer to the trichodermial palisade, especially in such cases where short and long hyphal members alternate, or the shape of the single elements of the chains change from one chain to the other, or in individual carpophores (Pl. XXVI, 3).

If the cortical layer is formed of radially arranged or, at any event, repent hyphae that are parallel to each other, it is called cutis (Lohwag, 1937, 1941) (Pl. XVI, 1).

Typical *Asterostromella* structure such as described for the genus *Vararia* (*Aphyllophorales*), is not found in the *Agaricales*; however, a limited *Asterostromella* structure such as is observed in the cortical layers of such aphyllophoraceous genera as *Campanella* and *Favolaschia*, has been observed in one agaric, *Asterotus dealbatus*. It should be known as a cortical layer of dichophysate structure. It is characterized by hyphae with short branches and secondary, etc., ramifications, all branching off under approximately right angles and at short distances, frequently causing a stellate appearance of the terminal hyphae. These elements are rather stiff, and more or less hyaline (Pl. XVI, 2).

In numerous species, the cortical layer is not or only slightly developed. In some *Russulae*, a dense gazon like covering of normal, very thin hyphae which are often forking or branching, reach the uppermost layer of the cuticle. They are otherwise not enough organized to call them a trichodermium. A similar, still less differentiated layer is found in the cuticle of some species of *Crepidotus*. In other species, such as *Panus conchatus*, the cuticular layer is merely denser as that of the stipe is often denser in a «rind», than the trama of the pileus. Such a structure is very frequent in the *Agaricales*, especially in the white spored families, and cortical layers of this type are called dense.

It should always be taken into consideration that certain types of veil (most conspicuously so the volva of *Amanita*; Pl. XVIII,2), leave a layer of fragments of not truly cortical origin on top of the cortical layers. When an analysis is made, care should be taken that these velar layers are not misinterpreted as being part of the cuticle. Such precaution can easily be taken by examining the structure of the veil first and substracting any layer of identical structure and origin from the layers of the cuticle proper.

The cortical tissue itself consists of one to three layers. If there is only one, we simply call it cuticle of the pileus (pellicle — it is viscid, and peels easily), and the covering layer on the stipe. If there are more than one, the uppermost layer in a completely developed specimen [13] is called epicutis. The epicutis may be a continuous layer in one of the types of structure named above (hymenium, hymeniform layer, trichodermium, epithelium, cutis, dichophysoid layer, or dense layer), or else it may consist of fragments of such a layer. In this case, the epicutis is the sum of dissociated but identical individual dermatocystidia, dermatopseudocystidia, « hairs », or any other type of bodies characteristic for this particular layer, and its origin in this case must be understood as conditioned by the rapid growth of an elastic (often gelatinized) supporting cuticular layer while the epicuticular layer stops developing at an early age. Such cases are not rare in the *Agaricales*, especially in such groups where the epicutis is the remainder of an early extension of the hymenium beyond the hymenophore, such as the epicutis of the *Russulaceae* (Pl. XV, 1), or at least many species of that family.

The epicutis is followed, downwards, or rather inwards, by a second layer, the hypodermium or subcutis. Though it seems illogical, general custom applied the term hypodermium, as a general term, for any structure between the epicutis and the context in most *Agaricales* (Fayod, 1889). In the species that have a cutis, the term subcutis is preferred by Lohwag (1937). Subcutis thus would become synonymous with hypodermium unless the term is amended to be any layer underneath the epicutis but confined to the cases where the cuticle consists of three layers, and then the upper layer (intermediate between the epicutis and hypodermium) is called subcutis,

[13] In *Agrocybe* and some other genera, the uppermost layer is detersile, and often washed off by rain or handling. It is therefore quite frequently missing in old or carelessly prepared specimens.

e. gr. in *Russula Puiggarii* where, underneath a well developed epicutis, a layer of hyaline gelatinized hyphae is followed, farther downwards, by a layer of pigmented, non gelatinized hyphae. In the author's opinion, the term subcutis should not be used in preference to the term hypodermium for any one (or supposedly one, i. e. considered as one by the observer) layer between the epicutis and the context of the pileus or stipe.

Lohwag in his original proposal (in Lohwag & Peringer, 1937) did not pay attention to the fact that he was dealing with two different categories: structures of layers, and layers. If the subcutis is understood in a revised sense, valid only for the naming of a layer, and not descriptive of its structure, the short cells immediately beneath the « hairs » or dermatocystidia of species with *Virescens* structure (see below), or of species with trichodermial palisade (as *Porphyrellus pseudoscaber*) should be called subcutis [11] (Pl. XVIII, 1, 4).

Another layer that does not necessarily belong to the cortical tissue, must be mentioned here. In some species of *Agaricales*, one can observe a layer of the context of the pileus that is differentiated from the rest of the context not morphologically but merely chemically or physically, i. e. it does not show the difference between the rest of the trama and itself unless it is exposed to a certain kind of radiation, or to certain reagents. This layer has been termed the subhypodermial layer of the context (Singer, 1942), in a discussion of the physical and chemical differentiation of this zone in certain species of the *Gomphidiaceae*. As another example, one may indicate the pigmented upper zone of the flesh of *Mycena iodiolens*. Yet, here it may be questionable whether the pigmentation is a purely chemical or physical character, inasmuch as it is not provoked by any chemical reaction other than the normal chemism of the developing carpophores in nature. It would therefore be better to call the pigmented zone of the context hypodermium, and the next following (upwards) zone — if any is present except the epicutis — subcutis; this solution, of course is possible only in such cases where the layer between the epicutis and the context is not definitely homologous with what is

[11] The subcutis would then, in many cases at least, be homologous with the subhymenium of the hymenophore. It might be inferred from what Lohwag & Peringer say about Fayod's term « cuticule proprement dite » that the latter was identical with what we call subcutis. This, however, is not the case since Fayod calls by this name either the epicutis or the hypodermium whichever is more developed.

otherwise consistently called hypodermium in the same group. It will therefore be expedient, though perhaps on a temporary basis, to maintain the term subhypodermal layer for a case like that of *Mycena iodiolens*. The same term may also be used for the zones of the context of the *Tricholomataceae, Resupinateae* that become gelatinized.

Gelatinizing of the hyphal walls whereby the hyphae become imbedded in a mucous mass — given enough moisture — is observed very frequently in the main cortical layers of the *Agaricales*, and the macroscopical consequence of such a condition is what is generally called a viscid or glutinous surface (pileus or stipe, or both). If such is the case, the cuticle is often called pellicle because of the easiness with which it can be peeled from the non gelatinous (or less gelatinous) layers. It must be kept in mind, however, that the separability (the peeling quality) may also hold for a non gelatinous cuticle that is separated from the lower layers of the trama by a gelatinous subhypodermal layer. The hyphal walls often gelatinize so completely that the walls practically disappear whereby the gluten becomes macroscopically homogeneous. Without the coherence due to the presence of the hyphae, the gluten often drops down, or is washed down, and the anatomical demonstration of such a specimen as having been glutinous or having had a gelatinous layer on or near the surfaces becomes very difficult or impossible. This is apparently the case in certain species of *Hygrocybe*, especially if herbarium material is examined.

A chemical difference between cuticular layers on one hand, and tramal layers of the context on the other hand, is often demonstrated by the iodine stain. This feature will be treated more exhaustively in the chapter on chemical characters.

In the discussion of the layers and elements observed in the cortical tissue of the *Agaricales*, we have not used the word hair so extensively as it is used by some authors. This word, when used as a term, mainly for differentiated terminal formations of hyphae in the epicutis, can often be replaced by the term dermatocystidia, or the more neutral expression « epicuticular elements ». However, if these elements actually resemble hairs there is no objection to calling them hair like hyphal ends (Pl. XXVIII, 1), and if the « hair » is actually a strand of hyphae, it may be called a hair like hyphal strand (Pl. XV, 3), or a pilose agglutination of hyphae, all neutral expressions. The author accepts the term hair only for those epicuticular elements

that are hair-shaped, form a pilose covering or down under a lens, and are not homologous with cystidia, cheilocystidia, pseudoparaphyses, or setae, or any other well-defined bodies. Such true hairs are found in all species of *Flagelloscypha, Lachnella, Crinipellis, Chaetocalathus*, and in some species of *Coprinus, Pseudohiatula, Mycenella*, and the covering that is made up by them is called pilose.

However, if the « hair » is much rather comparable to bodies that, as cystidia or cheilocystidia, or pseudocystidia, also occur in the hymenium of the hymenophore (even if the bodies occurring in the cortical tissue are slightly modified or if the corresponding body in the hymenophoral hymenium is absent in a given species, yet present in a closely allied form), the use of the word dermatocystidium recommends itself much more than the indiscriminate use of the word « hair ». For all these so called « hairs » the term can only be applied in the case that Romagnesi's (1944) thesis is accepted which differentiates between cystidial and pilose elements in a manner that is at variance with that adopted in the present book [illegible].

This also refers to the characteristic cells with apical appendages giving them a broom like appearance occurring on the pileus and sometimes on the edge of the lamellae in *Marasmius*, sect. *Hygrometrici* and some other species. The sterigmalike appendages and the palisadic arrangement as well as their occurrence on the edges of the lamellae in some species may suggest a hymenial origin, and this is also the author's guess. Since there is a good term in French literature (cellules en brosse) which can be adapted to other languages, we shall designate these bodies as broom cells in a category by themselves at least for the time being (Pl. XII, 2; XIII, 2).

In *Russula vesca* and species with similar elements (Pl. XVIII, 1) in the epicutis, we find an elongate erect epicuticular element in palisade that by Maire, Singer, Melzer & Zvara, Romagnesi, and other specialists has been referred to as « hairs ». It consists of a few basal cells which are rather short cylindric to sphaerocystoid, and the terminal member which is attenuate toward an obtuse or acute tip from a broader basis. More rarely a small appendage, which is usually more or less cylindric, is separated from the elongated cell by a sep

[illegible] « The cystidium... is a sterile cell ... characteristic for the basidia-bearing part of the hymenium » « The hair [« poil »] is a sterile cell ... which is originally characteristic for the covering layers [« revetements »] » Romagnesi, *Rev. Myc.* 9 (1): 6. 1944.

tum. With *Russula modesta* as an intermediate, this structure of the epicutis goes back to the so-called *Virescens* structure found in *Russula virescens, R. crustosa, R. Patouillardii, R. chlorinosma,* and the entire section *Plinthogali* of *Lactarius* (Pl. XVIII, 3 4). Here, the basal cells are more conspicuous, truly made up by erect chains of sphaerocysts, and ending up with a subulate or cylindric, rarely clavate or ventricose « hair ». In both the case of *Russula vesca* as well as in that of the *Virescens*-structure it is probable that the « hairs » are merely modifications of a transformation of some originally hymenial body. In fact, the acute cheilocystidia of some of these species are not basically different from the « hairs », and the short cells from which the latter originate can be compared with the subhymenial elements from which the cheilocystidia originate. Since the edge of the lamellae is not quite sterile, it is not difficult to see that these cheilocystidia have the same origin as the basidia. They gradually turn, however, into macrocystidia, since, for instance in *Russula crustosa,* already near the edge and on the edge many of the cheilocystidia have contents that turn blue in sulfovanillin, and farther upwards on the sides of the lamellae they become very voluminous and deep rooted true macrocystidia. Since we have a situation similar to that in *Marasmius* with its broom cells, it is necessary to provide a new term for these bodies, i. e. the terminal « hair » in the *Virescens*-structure as well as the « hair » in the epicutis of *Russula vesca.* This is necessary inasmuch as the use of the plain term dermatocystidia (which would otherwise be correct, may lend itself to confusion with what was formerly called dermatocystidium in the *Russulaceae,* i. e. the dermatopseudocystidium of macrocystidial or perphaps sometimes gloeocystidial origin. The « hairs » in the *Russulaceae* will therefore be called ciliate dermatocystidia in this book, a term that does justice to the homology established by Maire as well as to the rather descriptive name of these bodies, suggested by J. Schaffer (Wimpern, Cilien).

There is another term in *Russula* that must be mentioned here. In the velutinous and flocculose species, the hyphae forming the trichodermium or the trichodermial palisade, are often thickened, as compared with the narrow elements of the connective tissue, quite frequently multi-septate, yet, the single elements still remaining elongate and usually cylindric; they are incrusted, rarely apparently naked, slightly acuminate but rounded, or broadly rounded at the ends; they are colored (usually pale ochraceous). Melzer & Zvára

(1937) called these « hairs » in Czeck « vlakna primordiální » or « hyfy », Singer (1932) in German « Flockenhaare » ; Melzer and Singer agreed later to the term primordial hyphae which Melzer claims is used in the sense of Fayod. These primordial hyphae were later (misleadingly) renamed « Haare » (hairs) or « Fasern » (fibrils) by J. Schäffer (1934).

All these bodies in the *Russulaceae* can be distinguished according to shape and, to a certain degree, origin. However, here again, we find so called transitions already noticed by R. Maire (1907 and 1910) in which elements that morphologically seem to belong to one type of epicuticular bodies differ chemically, i. e. acquire macrocystidial character. This becomes a specific character in *Russula Peckii* where all so called « hairs », i. e. the ciliate dermatocystidia reveal bluing granules when treated with sulfovanilline. It would be, in the author's opinion, proper and descriptive to call this ambiguous organ « ciliate dermatopseudocystidia » [16].

For the benefit of those who have no experience with the use of all the terms applied to the cuticle and its elements, it must be emphasized that in enumerating and defining them, we are dealing with three categories and these categories should always be understood and clearly distinguished as such :

1. *Layers* : Velar layer, cuticle (pellicle); epicutis, below it the subcutis, below it the hypodermium, below it the subhypodermial layer.

2. *Structures of layers* : Hymenium (mostly in epicutis), or hymeniform layer, or trichodermium, or trichodermial palisade, or ixotrichodermium, or epithelium, or cutis, or dichophysoid structure, or dense structure.

3. *Elements of these layers* : Dermatocystidia, ciliate dermatocystidia, dermatopseudocystidia, ciliate dermatopseudocystidia, dermatopseudoparaphyses, dermatobasidia, differentiated hyphal ends, broom cells, hyphae of the fundamental tissue, hyphae of the connective tissue, dichophysoid hyphae, primordial hyphae, sphaerocysts, structure-less mucilaginous masses.

[16] These facts, taken from the anatomy of the *Russulaceae*, are especially instructive because of the thorough study that has been devoted to them by several authors whereby the knowledge of the anatomy of the *Russulaceae* was temporarily extended beyond our general knowledge in the *Agaricales*.

XIII. SPORES

In the *Agaricales*, uninucleate and binucleate oidia, conidia, and chlamydospores are comparatively less common than in most other orders of fungi. Only the chlamydospores of *Asterophora* have taxonomic importance as a generic character whereas the presence of conidia in other groups has ordinarily not more than the value of an auxiliary specific character inasmuch as the conditions under which conidia are formed in nature, their constance, and even their existence in many species are unknown (see Brefeld, Vandendries and others on *Coprinus*).

In *Asterophora*, the chlamydospores (Pl. X) arise from the binucleate phase of the fungus, more precisely from the upper portion of the pileus or the hymenophore and also from the binucleate mycelial hyphae. These portions of the fungus become pulverulent, and, at the same time, the hymenophore and the production of basidiospores appears to be suppressed to a certain degree. However, basidia and basidial spores are formed in both the known species, and they have even been brought to germination by Brefeld (1889). The resulting mycelia often disintegrate into oidiachains. The chlamydospores can also be obtained in culture; they are formed predominantly intercalarly in *A. parasitica* where they are smooth, and predominantly terminally in *A. lycoperdoides* where they are coarsely stellate echinate; the chlamydospores have been made to germinate by various authors, and even carpophores have been obtained in culture (Thompson, 1936). It is now amusing to look back at the classical controversy between those who attributed the chlamydospores to the agaric and those who wanted to see in them an ever-present parasitic Fungus Imperfectus.

As for the arthrospores of *Armillariella ditopa*, see p. 28.

The main form of propagation in the *Agaricales* is by the way of anemochoric basidiospores [47] which are formed by the basidia of the hymenophoral hymenium; a small minority in a few species is formed by dermatobasidia and these spores are, in all cases investigated thus far, identical in all respects with the spores formed by the basidia of the hymenophoral hymenia. The hymenia sporulate through

[47] In papers on *Agaricales*, the word spores customarily refers to the basidiospores; the latter, more exact term is very rarely used.

out the mature life of the carpophore in the fleshy forms but are frequently found in a non sporulating stage (inaccurately, these carpophores are usually referred to as sterile). This is much like the conditions in the tough and leathery *Aphyllophorales*, especially the *Microporus-Daedalea* group, and the *Stereaceae*. These long lived (though in the *Agaricales* always annual) carpophores «time» the sporulation period or periods in accordance with the weather conditions and the seasons. For the practical purposes of spore study, the genera of the *Tricholomataceae Lentineae*, the genus *Trogia*, and the genera *Marasmiellus*, *Marasmius*, *Crinipellis*, *Chaetocalathus*, and *Collybia*, are most annoying. Otherwise, the spores are always present in smaller or larger number though often not in sufficient number to produce a spore print. The examination of the spores from spore prints is preferable to the examination of the spores found in fragments or sections of the hymenophore. The spore print contains only mature spores, and it is then not necessary to fall into the habit of measuring only the largest spores (as was done by Bresadola) in order to be sure to exclude immature spores, and also of measuring all spores, excluding the very smallest and the very largest (as was done by Lange). These methods will invariably, in an average, yield too large, or too small measurements which can be demonstrated if the measurements obtained by these methods are compared with those obtained by measuring all sizes of spores from a spore print [11]. Not only the measurements will be exact, it will also make it impossible to create nomina ambigua by studing the hyphae of one species and the spores of another as has sometimes happened when a large amount of foreign spores (even mould spores — incredibile dictu) was blown on the hymenophore of the specimen under examination while it was in the basket or in situ.

In shape, the basidiospores vary from almost perfectly globose (Pl. XIX, 2; XXIV, 1) to strongly elongated, from round to nodose (Pl. XIV, 2), stellate, or angular (Pl. XII, 5-6) in circumference, and from terete to laterally compressed (Pl. XI, 4) or angular (polyedric) when seen from one end (the longitudinal axis toward the objective of the microscope (Pl. IX). They are never perfectly orthotropic (Corda

[11] R. Maire also enumerates other sources of errors in spore measuring (comparison of measurements in different media, faulty use of the ocular micrometer, etc.) in a paper that will be very helpful for those in need of more elementary advice in techniques (*Bull. Soc. Myc. Fr.* **42**: 43-50, 1926).

1842) and equilateral, a feature common to almost all spores produced on the outer surface of carpophores in the *Basidiomycetes*, and often put in contrast to the symmetry of spores produced by angiocarpous (endocarpic) forms. This can be explained by the manner in which the spores are produced and discharged at the tip of the sterigmata. A study of the spore discharge in non angiocarpous *Basidiomycetes* shows that the inaequilateral spore is advantageous in spore discharge, or at least a logical by product of the exogenous discharge [22] whereas in angiocarpous *Basidiomycetes*, the spores are disseminated through a final disintegration (partial or entire) of the peridium, or by other devices, after the basidia themselves have collapsed and disappeared in the gleba. The spores are consequently freed from the sterigmata by the disintegration of the basidia rather than by forceful discharge, and they are not in need of any lever-action or any other advantage gained by the asymmetry (or heterotropism, Corda, 1842) of the spores so general in the non angiocarpous forms. While all this is obviously basically true, the further statement that, therefore, all *Agaricales* have heterotropic spores, and all *Gastromycetes* orthotropic spores is not a law without exceptions. In the first place, the spores of most *Gastromycetes* (the author has studied in this regard *Secotium* and *Torrendia*, are not all perfectly orthotropic, but some spores are always heterotropic because of the lower or more oblique position of the sterigma on which they were produced. Furthermore, the gastroid form of *Boletinus decipiens* which, biologically speaking, is a Gastromycete rather than a bolete, has truly heterotropic spores. Some *Russulaceae* that are otherwise close to certain *Gastromycetes* of the group called *Astrogastraceae* by French authors, and form their spores either gymnocarpously or pseudoangiocarpously, have spores so close to truly globose that it is very difficult to establish whether they are inaequilateral while still being slightly obliquely attached by their hilar appendage which makes for a certain degree of heterotropism (Pl. XIX, 2). This « almost orthotropic » manner of spore formation cannot otherwise be explained than by the affinity of these species with true *Gastromycetes*. Orthotropism and heterotropism of basidiospores are, consequently, not a character of immediate adaptation to either angiocarpous development of the

[22] See the various theories given on spore discharge in *Basidiomycetes* by Buller (1924), Ingold (1939), Lohwag (1941), Prince (1943), Corner (1948). It appears that the mechanism (septation, etc.) varies in the different groups

carpophores or to non angiocarpous spore production even though historically and evolutionally, the manner of development appears to be the source of this divergence of spore development.

The strong inaequilaterality of the spores of many *Agaricales* makes it easier to differentiate between an inner (often flatter or even depressed) and an outer (often more ventricose) side of the spore; in elongate spores, these sides are distinguishable to the right and left of the longer axis. The hilar end (base) of the spores is oblique and the hilar appendage (part of the spore that joins the tip of the sterigma) is nearer the inner side than the outer side. It lies in the direction of the geometric axis of the spore only if seen from the inner or the outer side. If the spore is turned around the geometric axis by 90°, i. e. when seen in profile, the hilum becomes somewhat removed from the geometric axis. On the other hand, the apex of the spore is always on the distal end of the geometric axis of the spore. In spite of its inaequilaterality, the spore has in most cases approximately the same breadth whether it is measured from the inner side to the outer side, or seen in profile (i. e. tangentially — if the 4 spores are thought as four points in a circle). This means that the smaller diameter is almost identical in all positions the spore may take when it turns around its axis as often happens when the spore moves in the medium of a temporary preparation. There are, however, exceptions to this rule. The genus *Deconica* is especially notorious for its spores being narrower in profile, and broader (about 1-2 µ) when turned around on their axis by about 90° (i. e. to a point where the position of the hilum coincides with a continuation of the geometrical axis and the spore is seemingly symmetric; Pl. XI, 4). Such spores are called lentiform in spite of the fact that they are not subcircular in circumference but rather oval. Lentiform spores also occur in *Conocybe* and in *Coprinus*, but here, the character has no more than specific value though Fayod proposed a separate genus for those *Coprini* that show it. It is remarkable that most lentiform spores are slightly to distinctly rhomboid, i. e. they have an inaequilaterally hexagonal outline (shape of benzene ring formula) in frontal view.

The inner side is either convex, or flattened (Pl. XXV, 4, 11); or

[24] This is one safe way for the beginner, to make sure which end of the spore is the apical, and which the basal end when the spore is detached from the basidium

depressed, especially in the region just above the hilum, or in the lower half. We therefore speak of spores as having (or lacking) a suprahilar applanation, or a suprahilar depression.

The elongate spores are called ellipsoid (Pl. XXVIII, 3 *h i*) or ovoid if their Q (length divided by breadth) is smaller than 2; otherwise, they are called ellipsoid-oblong (Pl. XXVIII, 3, 6), fusoid (Pl. XXVII, 3-4) or cylindric (Pl. XVI, 8), more rarely (especially in *Marasmius* and *Tylopilus*, sometimes *Boletus*) clavate with the club-end beneath. Cylindric (rarely fusoid or ellipsoid-oblong), white or pale-colored spores are characteristic for wood-inhabiting species (yet, of course, by far not all xylophilous species have cylindric spores), and even more for a certain tribus in the *Tricholomataceae* (*Lentineae*) where this shape is a tribus character.

Among the species with angular spores, Romagnesi distinguished two types, a symmetric and an asymmetric type. Usually a good indication of symmetry (Pl. XI, 5 6) is the presence of a right (90°) angle at the lower end of the spores when the spores are seen frontally (i. e. with the hilum in line with the geometric axis), whereas in asymmetric spores, the lower end forms a larger angle [1]. Since these two main types are known to exist — along with a series of subtypes — only in a single genus, *Rhodophyllus*, we refrain from a more detailed discussion of this problem.

In two genera the spores are visibly angular only in « upright » position, i. e. if seen from one end, with the longer axis of the spore vertically pointing at the objective. The sides between the angles are, in this view, either plane or slightly concave, and the number of angles varies from 5 to 10 (it is most frequently either 6, 8, or 10). When seen in profile or in frontal view with the long axis being horizontal, these spores hardly show much unevenness and will easily pass as smooth (*Clitopilus*, Pl. IX; XXVII, 8 9) or warty rough (*Rhodocybe*) unless the angles are slightly projecting into subulate striae. This character is of an undeniable importance in the taxonomy of the *Rhodophyllaceae*, and has also been observed in spores with « removed » [2] ornamentation of *Melanoleuca* (*Tricholomataceae*).

[1] For a more thorough understanding of Romagnesi's spore types, it is necessary to study his paper, *Bull. Soc. Myc. Fr* 53: 319-338. 1937.

[2] This means with the amyloid exosporium dissolved according to the method employed by Josserand (1941).

The walls of the spores are either smooth or ornamented. Locquin (1942) distinguishes 3 types of ornamentation, viz.

1. *The primitive ornamentation (ornementation primitive).* It disappears soon because of the growth and the further differentiation of the wall, and leaves usually no traces on the mature spore. Locquin who is inclined to think that it may be interpreted as phylogenetic reminiscence, suspects that possibly certain ornamentations of little developed species might go back to this origin. If so — and the thoughts of Locquin are theoretically not incorrect —, the author cannot see why the primitive ornamentation in this case does not become identical with the secondary ornamentation which is the persistent and final one. If only one persistent ornamentation exists, there seems to be little to gain by calling it any more technical names than simply — ornamentation. The primitive ornamentation has been discovered in *Macrolepiota procera* where the mature spores are completely smooth; it does not exist in the majority of the species of *Agaricales.*

2. *The secondary ornamentation (ornementation secondaire, definitive).* This is said to be the final persistent ornamentation originating in the episporium, the exosporium, or the endosporium, i. e. in any of the layers of the spore wall proper (not in the perisporium). However, Josserand, two years earlier, has distinguished the fundamental ornamentation in the *Russulaceae,* which excludes the exosporial ornamentation that is of later origin and should be known as secondary ornamentation if this latter term were applied at all (the author prefers the term «exosporial ornamentation»).

3. *The perisporial ornamentation (ornementation perisporique, evanescente).* This is of perisporial origin (for the term perisporium, see below, p. 70, 71), and is fugacious, becoming ruptured into patches and warts much in the manner the volva of an *Amanita* is ruptured and finally obliterated by dissolution or lack of elasticity.

This classification of the ornamentations cannot at present be applied in all cases because it requires very exact studies of the fine structure of the walls and their metachromatic properties against a series of dyes and reagents, as well as a study of the development of the spore from its first appearance at the tip of the sterigma till maturity. Consequently, in many cases, it is wise to speak of ornamentation in the general sense of the word. In contrast to the anatomical ontogenetic classification it is always possible to apply the classification of typical configurations of the spore ornamentation in the

Agaricales[1]; these configurations are marked with Roman numbers.

Type I. Coarse banded ridges form a reticulated surface *(Strobilomyces floccopus, Boletellus retisporus, Lactarius lilacinus).* (Pl. XIX, 2; XXIV, 2, lower spore).

Type II. Ridges and fine lines and warts form a reticulated surface *(Russula Mariae).*

Type III. Warts or spines connected to form a reticulation.

Type III a, which signifies a complete network as in *Russula emetica.*

Type III b, which signifies an incomplete network.

Type IV. Warts or spines connected by scattered thin lines, not forming a reticulation or a fragment of a reticulation. (Pl. XXIV, 6, lower spore).

Type V. Warts or spines from which short, thin lines run over the surface of the spore wall but do not reach the nearest wart or spine. (Pl. XXIII, A, 1).

Type VI. Warts or spines completely isolated *(Russula Schiffneri, Laccaria echinospora).* (Pl. XXIII, A, 2, 4, 5).

Type VII. Punctations and fine, short lines, sometimes touching or crossing each other *(Russula mellioleus).*

Type VIII. Catenulate warts usually crowded into or connected to chain like rows *(Russula elephantina).*

Type IX. Ornamentation continuous, a smooth surface resulting (young spores of *Russulaceae, Fayodia bisphaerigera).* (Pl. XI, 1).

Type X. Longitudinal ridges, often slightly spiralling, often somewhat anastomosing *(Boletellus Russellii,* Pl. XXIV, 9; anastomosing : *B. ananas,* Pl. XXIV, 7).

Type XI. Short warts or cylinders perforating a heterogeneous wall but scarcely projecting *(Porphyrellus gracilis, Boletellus betula, Crepidotus,* sect. *Echinosporae, Tubaria thermophila)* (Pl. XI, 2; XXIV, 4-5).

Type XII. Surface irregularly warty roughened (*Lepista nuda Linderomyces lateritius).*

In descriptions, the use of the figures designating the type of ornamentations, or a number of these figures combined (the unusual ornamentation in a species given in parentheses) shortens the descriptions considerably while still maintaining a high degree of pre

[1] In other fungus spores, more types have been distinguished (short-ridged, loculate, etc.).

cision, and is generally recommended, especially for those groups that, like *Russula* and *Lactarius*, have a great variability in spore ornamentation according to species, subspecies, varieties, individuals and individual spores. This scheme of ornamentation types is not concerned with the fundamental nature of the ornamentations, i. e. with the questions by which layer and by which process in the development the ornamentation of the spore is formed. Isolated warts in a spore layer beneath the outermost layer in *Fayodia bisphaerigera*, isolated spines in *Russula Schiffneri*, and innate (fundamental) spines in *Laccaria echinospora*, all correspond to the definition of type VI, yet the chemical character, the development, and the homologies of these ornamentations are by no means identical [33].

The spore wall is in many cases simple or seemingly simple (Pl. XXVIII, 3) i. e. under the prevailing method of investigation, it cannot be recognized as double or complex. In the *Agaricaceae*, and in the related dark spored families, the spores often consist of two or three layers, easily distinguishable in ammonia, KOH, or Melzer's reagent, and in cresyl blue solutions. These layers have a varying relative diameter. The inner layer is called the endosporium [34] (De Bary, 1884) (Pl. XIII, 1; XXIII, B, 2, 5); the external layer is called the episporium (De Bary, 1884, (Pl. XIII, 1, XXIII, B, 2, 5). Sometimes there is an intermembranal layer or what appears to be an intermembranal space (*Chlorophyllum molybdites*), and in some species (*Macrolepiota procera*), the endosporium has two layers, the internal and the external endosporium (Locquin, 1942). In other instances, there is a third, often ruptured or saccate structure present that envelops the whole spore like a bag, or fragments of a hyaline covering. This part of the spore is called the perisporium (Pl. XI, 1). It is very evident in such forms as *Galerina Hypnorum* forma *montana* or *Strobilomyces floccopus* (Pl. XXIV, 1), in the latter case strongly reminiscent of what is known in *Scleroderma cepa* and other species of that gastromycetaceous genus. Even in *Russula* (e. gr. *Russula archaea*) such enveloping layers have been noticed. Lohwag (1937) thinks that they result from the outer part of the

[33] More data on the spore development and the micro-structure of the spore walls and ornamentations can be found in Locquin's papers on this subject (see literature).

[34] It is important to distinguish between two similar terms: endosporium — the innermost wall of the spores, and endospore — a spore formed endogenously inside an ascus or sporangium.

basidial sterigmatic wall which is usually either so closely agglutinated, or so fugacious that no trace of it can be seen in mature spores.

In the literature, there is also indicated another term, exosporium. The exosporium was first given by the pre-Fayodian authors, e. gr. De Bary, as a synonym of episporium. However, the word episporium was preferred. Fayod himself, unfortunately mixed up the terminology as has later been shown by R. Heim (1931) *. What Fayod called exosporium is a layer outside the episporium. In some cases, Fayod may have taken the optical halo as an outer layer, as was suspected by Heim but Locquin has proved that a true exosporium in the sense of Fayod actually exists in many cases, and that this exosporium had thus far escaped the attention of all authors except Fayod. There can be no valid reason to prefer Fayod's terminology to the use of the term episporium in the sense of De Bary and the French authors (starting with Patouillard), and the term exosporium in the sense of Fayod and Locquin

Consequently, in the most complex spores known, we have to distinguish between the following layers of the wall and its outer envelopes (from inside outward):

1. The internal endosporium.

2. The external endosporium: both colorless, usually thinner than the episporium, or equally thick, sometimes absent (in monostratous spore walls).

3. The episporium: in the colored spores, this is the pigmented portion of the spore wall; in hyaline spores, it is always the thickest layer of all, and frequently shows an ultrafiltering capacity for cresyl blue in watery solution. It is doubtful but possible that the episporium may also be composed of two layers in a few species (see Heim, 1931, and Locquin, 1943).

4. The exosporium: this is colorless and consistently thinner than the episporium, usually delayed in its dissociation from or deposition on the primordial episporium, often of different chemical structure as compared with the neighboring strata (perisporium and episporium)

5. The perisporium: a loosely attached non-pigmented layer that envelops the spore as a bag, or a closely attached but fugacious layer

* What Fayod calls endosporium is not the endosporium of De Bary and of the modern anatomists but the episporium of De Bary and the French mycologists, a term adopted in this book The true endosporium is called « la couche membraneuse du protoplasma » (Primordialschlauch of the German authors) by Fayod.

that is destroyed by dissolution or fragmentation in an early stage of the spore development. It is doubtful but possible that there are occasionally two sub-strata composing the perisporium (see Locquin, 1943).

These anatomical facts and discussions of terminology are not of a remote significance for the taxonomist but of primary importance. The spore, with all its characters, has become, more and more, one of the most important characters on which the taxonomy of the *Agaricales* is based. The descriptive data become simpler and more definite when they are based on exact anatomical observations, and the homologies become more evident. Comparison between the spores of different species must be based on the comparison of homologous parts of the spore. The consecutive observations of Malençon (1929, 1931), Josserand (1941) and Locquin (1943) have shown that the *Russulaceae* have a fundamental ornamentation formed by the episporium which is slightly colorable with Melzer's reagent; the zone above the hilum and the larger portion of the surfaces of the fundamental ornamentation are covered with a thin exosporial ornamentation which is disrupted and clings to the episporium by a certain adhesiveness of its own and an increased readiness for humectation of at least parts of the episporial surface, and it responds chemically to most tests for amidon. It can be dissolved by several chemical substances, such as concentrated HNO_3, and less uniformly by NaOH, KOH, etc. in a heated concentrated solution. Thus, Josserand first bared the fundamental ornamentation of the *Russulae* and *Lactarii*; but in *Leucopaxillus pulcherrimus*, after dissolution of the amylon-layer, he did not find any fundamental ornamentation; neither did the author on the related *L. albissimus*, using concentrated nitric acid. This means that the entire ornamentation of *Leucopaxillus* (at least those two species) is superficial, heterogeneous, and exosporial. Josserand indicated for *Melanoleuca* that the fundamental ornamentation is likewise either absent or insignificant. This marks a difference between the *Russulaceae* and the *Melanoleuca-Leucopaxillus* complex which is most important considering the elongated spores of such species as *Russula heterospora* and *R. ventricosipes*, and their similarity with those of *Melanoleuca*.

It may be noted here that the ornamentation of the *Russulaceae* has been thought to be, in its entirety, of destructive origin, i. e. a layer, at first continuous that because of the growth of the episporium breaks into more or less regular fragments. Josserand exempted the

fundamental ornamentation from this rule but thought it still applicable for the exosporial ornamentation. However, Locquin offers a new hypothesis on the development that is a physical one : As the exosporium solidifies at a certain point in the maturation of the spore, it cannot cling to certain areas because of the physical differences which, according to Locquin are determined by the different organization of the micelles of the surface of the episporium. Whatever the fate of this explanation may be, it must be admitted that it is the only one that is in full agreement with all the facts available. It does not by any means invalidate Malençon's now classical series of spore configurations in the « Asterosporées » i. e. the bridge between some *Gastromycetes* and some *Agaricales* ; leading from the *Hydnangium carneum* group to the *Russulaceae*.

The warty spores of the *Cortinariaceae* have not been studied equally carefully and by an equal number of observers in recent years, and one might assume that here the development of the ornamentation is, in the great lines, similar to that of the *Russulaceae*. However, unless more comparative anatomical ontogenetic and microbiochemical work supports this analogy by more facts, it would be a wise course to refrain from taking the obvious homologies for granted. Yet, the spore ornamentation of *Galerina* (*Cortinariaceae*) has a character in common with the *Russulaceae* that is of great importance in any discussion of the ornamentation in these genera, and also of a significance in taxonomy that can hardly be exaggerated. This is the round smooth (or comparatively smoother) area just above the hilar appendage on the inner side of the spores which we may name suprahilar disc. If this disc is amyloid, it is termed hilar spot (tache, Heim, 1938), so in *Melanoleuca* and the *Russulaceae* ; if it is not amyloid and merely stands out by its smoothness (well visible in NH_4OH preparations imbedded in Shear's mounting fluid or with the ammonia replaced by a 50 p. c. watery solution of chloral hydrate, it has been called plage (Pl. XII, 3) by Kühner (1926), and this term has been adopted without change in other languages than the French. The plage is the most important character distinguishing the typical *Galerinae* among the *Cortinariaceae*, and the hilar spot is one of the most important characters separating *Melanoleuca* from *Leucopaxillus*.

The wall and its layers are continuous in many species, in others, especially those with complex walls, the spore wall is partly or entirely interrupted or modified at the apex. This apical interruption or modi-

fication is either (1) a germ pore (Pl. XI, 2; XI, 4; XIII, 1; XXIII B, 2, 5), i. e. an interruption of the outer layers of the wall with the endosporium either intact or also modified to interrupted (examples: *Macrolepiota, Kuehneromyces, Bolbitius,* etc.) whereby the apex of the spores often becomes truncate if the interruption is broad enough, or (2) a callus, i. e. a thinner walled apical region that is more or less convex, or even callously protracted rather than truncate (example. *Galerina* spp.). The callus has been named by Heim (1931) who first distinguished it from the germ pore with which it was often confused before (Fayod, 1889) provided it was noticed at all. The germ pore has been known for a long time but its taxonomic importance has been stressed only by Fayod and Patouillard.

The germ pore of light colored spores is not always easy to recognize under dry objectives, and sometimes even under immersion lenses. It should be studied after an initial treatment with 10 p. c. KOH which is subsequently removed, and replaced by cresyl blue solution (see p. 77) or aceto-carmine.

The microscopical basis of the macroscopical difference in spore print color is usually the pigmentation of the spore wall (see p. 16, 105); most of the dark spored families can be recognized from the spore color under the microscope; however, the cream color, greenish and pink shades in light spored agarics and boletes are not always clearly reflected in the color seen under the microscope. Sometimes, the pigmentation of the spores under the microscope is of independent value in the taxonomy of certain groups (*Xanthoconium stramineum*; *Callistosporium*, etc.).

The size of the basidiospores ranges from 2 to 40 µ in length and accordingly in volume. All spores are unicellular, except for a few isolated cases where the old spores have been seen to become septate (*Crinipellis mirabilis*, etc., Pl. XXVIII, 3 *d-e*) after discharge. Heim (1948) interprets this as a direct transformation of the spore into a binucleate chlamydospore.

The spores are never sessile on the basidia in the *Agaricales*, in spite of Fayod's indication of sessile spores in his genus *Astylospora* which seems to be based on faulty observation. They are always borne on the apex of sterigmata that are apical and half-sickel shaped or horn shaped (Pl. XII, 1; XXIV; XXV, 3; XXVI, 5; XXVII, 2, 6, 10) in the *Agaricales* (very rarely lateral, a feature that has no taxonomic significance since it is an individual irregularity in an occasional basidium).

The protoplasmatic interior[27] of the spores is usually colorless; it often includes one to several oil-droplets[28] (Pl. XXVIII, 3 e) which are of much less taxonomic value than in the *Discomycetes*.

XIII. STAINS, MACROCHEMICAL COLOR REACTIONS AND CHEMICAL ANALYSIS

Absorption of specific dyes is not a direct expression of the chemical constitution of the various parts of the plant tissue, yet in certain cases, the absorption of the dye is different in different organs and different in different parts of hyphal or sporal walls, etc. This so-called metachromatism is not the same in the same organs of all *Agaricales*, and Kuhner, Singer, and Heim have recently used this fact as the basis of taxonomic as well as organographic differentiations, i. e. for the characterization of groups in the classification of the *Agaricales* and for the characterization of certain specific types of organs. These metachromatic colorations like the chemical reactions which also have been introduced into agaricology in recent years, are only characters, and are not pretended to be more than that. Some authors speculated on the chemical nature, and the physico-chemical conditions under which these selective colorations and color reactions take place; in some instances, the substances involved have been studied to a certain degree, from a chemical point of view, or else the type of reaction taking place was too obvious to be overlooked by the mycologists, yet, as a rule, no systematic attempt has been made to identify the reacting substances by a standard method of chemical analysis, and to explain the reactions taking place in a biochemically proper manner. The notable exceptions that might be mentioned here are the poisonous agents in a very small number of poisonous fungi, especially *Amanita*.

This, in the opinion of most modern mycologists employing chemical characters, does not render them any less valuable from the taxonomic point of view. The only requirements of a good character are its constancy and correlation with other characters. Those who have in the last 20 years systematically introduced new chemical characters had only two preoccupations: (1) are the reactions obtained genotypical or phaenotypical and accidental, i. e. are they reactions typical for

[27] « nucleus » of Corda (1842).

[28] « nuclei » of some authors.

the form under consideration, or dependent of factors such as temperature, substratum, or host, and consequently irrelevant for taxonomic purposes; (2) are these reactions correlated with morphological characters?

Even if the chemical substances involved in the reaction are unknown, or the modus of their transformation hypothetical, their taxonomic value may thus still be considerable, and arguments in questions of systematics based on chemical characters may still be valid provided that the chemical character is both genotypical and correlated with morphological characters.

This does not mean that an investigation of such reactions from a purely chemical point of view be omitted in the future. It is quite obvious that work of this order is highly desirable. An attempt has been made to correlate both taxonomic and chemical research in lichenology especially as far as the isolation and identification of lichen acids were concerned, and the results have been interesting and valuable both from the chemical as from the taxonomic point of view.

The only objection that may be made to the taxonomic use of « good » chemical reactions as characters in spite of the lack of a chemical explanation of the changes observed, is that an equal external effect may be obtained by using the same method with different species even though the substances involved may be different. The error in our interpretation would then be the application of a term such as « positive » or « amyloid » for a reaction of a certain order in all cases whether they are due to the presence of an identical substance or merely of a substance with identical or similar reaction in contact with a given reagent. It is, of course, probable, or almost certain, that the amyloidity of spore ornamentations or spore walls is not based on the presence of the same substances in all cases where a «positive» reaction with an iodine reagent is obtained. In fact, the apices of the asci of certain *Ascomycetes* (pure blue reaction with Melzer's reagent), the ornamentation of the spores of the genera *Melanoleuca* and *Leucopaxillus* (blackish violet), the hyphae of *Marasmius* and *Mycena* (vinaceous to vinaceous brown), and the hairs of *Crinipellis, Chaetocalathus, Lachnella* and *Merismodes* (brownish violet to deep reddish brown), the spore walls of *Neohygrophorus angelesianus* (pale greyish livid, and perhaps some more « amyloid » walls, are probably of a different chemical composition, and the amyloid reaction is not caused by the same substance, or the same groups of substances.

All this may be true. Yet, if an argument concerning a taxonomic question, and based on chemical characters, is only one part of a series of reasons that support, for example, the affinity of two groups, the chemical character should not be disregarded on theoretical grounds. The overemphasis put on a chemical character alone (e. gr. in Melzer & Zvára's monograph of the *Russulae*) is not justifiable even if the chemical identity of the reactions in each case could be demonstrated by analytical means. This does not make the discoveries of Melzer & Zvára any less valuable for the use by an experienced taxonomist. Those who reject chemical characters must also reject color, odor, taste, and gelatinosity which are likewise characters without a fully explored chemical basis in most cases. We would then have to rely on morphology alone — and morphology, at present, does not provide complete guidance either. It is therefore necessary to use, with the utmost caution, but without blind reluctance, all available characters, the more — the better. Biology is not yet a strictly exact science, and asking to consider it as such without allowing for a large number of working hypotheses, is equivalent to stopping its development.

These observations are necessary in order to introduce the use of chemical characters to a broader public than has ever been done before. The acceptance of chemical characters as a valuable contribution to the factual material available for the determination of affinity is not in danger since even the critics of this new method make widest use of it in their own papers. However, unreasonable criticism is merely another factor in delaying the broader application of chemical characters among the mycologists, including collectors data and routine determinations.

Metachromatism with cresyl blue

Cresyl blue mounts of spores of *Macrolepiota*, *Leucoagaricus* and *Leucocoprinus* allow the observation of the endosporium because of a selective coloration that results from ultrafiltration of the dye solution by the episporium in such a manner that the endosporium is dyed reddish, and therefore stands out enough to be rather conspicuous even in cases where it is not very strongly developed. In other genera of the *Agaricaceae*, the endosporium — whether strongly developed or not — does not show such an effect in cresyl blue mounts. This differentiation has been shown to be of great help in the subdivision

of this family, as an additional spore character to be used together with the iodine reaction and the germ pore.

In the hyphae of the stipe, cresyl blue often provides a similar character based on metachromatism which is somewhat but not quite parallel with the Melzer reagent's metachromatism (see p. 79). Kühner who has discovered both the sporal and the hyphal metachromatism in cresyl blue-sections enumerates several important differences between the positive reaction with the Melzer on one hand and the metachromatism with cresyl blue on the other hand (1933). This makes the use of cresyl blue in addition to that of the Melzer even more important. The sections can be treated with ammonia or KOH at first in order to separate the hyphae, but the alkaline solution must be removed entirely afterwards; the section is then colored with a watery solution of cresyl blue, the excess dye is removed with filter paper, and replaced by water. In certain species such as most *Mycenae*, many *Marasmii*, etc., the hyphae of the stipe become red, thus contrasting with the normal coloration of hyphal walls obtained with cresyl blue which is a pale violet, pale blue, or practically nil. The cortical layer of the stipe should be disregarded for this purpose.

A strong deep blue stain is obtained by the use of cresyl blue on the interior of all gloeocystidia, in the *Corticiaceae*, *Cantharellaceae*, *Leptotaceae*, and in the agarics (Pl. XXI, 3); this characteristic metachromatism is, as we have seen above, a perfect means for recognizing these bodies in dubious cases (Singer, 1945; Heim, 1946). The technique is the same as described above.

Kühner has also indicated (1934) « very numerous precipitations of a bright red color » in several Hygrocybes (especially the species with viscid stipe) which is not generally observed in other fungi; the walls of the cystidia are colored either metachromatically (deep lilac or violet, or the same color but very pale, Pl. XXI, 4), or blue (*Inocybe*, Pl. XIV, 2; XVII, 1); reddening (metachromatic) trama is found in most of *Agrocybe*, *Hygrophorus*, all *Mycena*, *Lepiota*, and *Hebeloma* species studied by Kühner, never in *Cortinarius*, *Inocybe* or *Naematoloma*; strong reddening of the trama of the *Amanitaceae* is observed in the subgenus *Eu-Amanita* (excepting the *Phalloides* group), and in the *Emetica* group of *Russula*, the basidia are distinctly metachromatic in many agarics (*Tricholoma*, *Cortinarius*, and others) but never in the *Boletaceae*.

Cresyl blue can also be used in order to study the ornamentation

the same way as is done in the *Russulaceae* with Melzer's reagent; cresyl blue has given a picture surprisingly similar to an exosporial ornamentation of the type III b-IV (V) in *Russula*, when used on spores of *Neopaxillus echinospermus*. The exosporial ornamentation of the *Cortinariaceae* is also deep violet colored but usually less well differentiated from the episporium, at least optically.

Cresyl blue is not the only dye that provides the anatomist, working on *Agaricales*, with metachromatic colorations. Several more (cotton blue, diamine blue, alkaline methylene blue, various violets, carmines, etc.) metachromatic stains are known, but their use has not yet become taxonomic routine.

This brings up the question which dyes are recommended for general use in *Agaricales*. For routine preparations of an unknown agaric or bolete, it is customary to use ammonia mounts [**] first without any dye: it is not wise to start the study of a species with stained material. Only as a second step, in order to get clearer pictures, this same preparation may be dyed with phloxine (now generally used by American specialists of *Aphyllophorales*), 2 p. c. alcoholic solution, which is stable in ammonia or even KOH mounts. Phloxine is, however, taken up by the interior of the hyphae rather than by the walls, and for the walls, cresyl blue is as good as any other dye for a first try. As a rule, every fungus and every organ, and even every part of this organ require individual stains, according to their chemical constitution and physical properties. In many cases, chemical reactions will be used, such as Melzer's reagent, in preference to organic dyes.

Micro-chemical reactions

It is difficult to differentiate between dyes and reagents since many reagents, among others the most important reagent for the study of *Agaricales*, Melzer's reagent, act rather by absorption than by fully measurable chemical transformations of the treated material. However, even though the Melzer reagent is, in a certain sense, an inorganic dye causing metachromatisms of the same order as cresyl

[**] KOH is preferred in tough species or in species with dense tissue that are not mercerized easily by NH_4OH, also in preparations that are intended to show the general structure of an organ, as in KOH strong pressure on the cover glass can be avoided. However, for a study of fine structures such as diverticulation of epicuticular hyphae, pigment incrustations, and spore ornamentations, KOH is definitely inferior to NH_4OH.

blue, it is currently considered as a reagent rather than a dye. It was unavoidable to mention the Melzer reagent in the preceding chapters, but we shall now attempt to give a resumé of the reactions that can be obtained with it.

The reagent has completely replaced the use of any alcoholic iodine solution and the classical use of $Zn\ Cl_2\ J_2$. Its composition though slightly altered in one sense or another (without much difference in effect) by some mycologists is still the original indicated by Melzer (1924).

KI	1.5 gr
Iodine	0.5 »
Water .	20.0 »
Chloral hydrate . .	22.0 »
	44.0 gr

It has first been used on the exosporial ornamentation of *Russula*, and this was its original purpose. However, the mycologists who later searched for all kinds of positive iodine reactions in the tissues and spores of the *Agaricales*, found in Melzer's solution a convenient standard solution that would always give identical results if applied in an exactly circumscribed manner. It cannot be emphasized too strongly that any deviation from the formula and the following procedure, may (not must) cause a discrepancy between the results obtained and those described by the authors. In the first place, it makes no difference when the material has been collected and in what manner it has been dried. Material about 120 years old still reacts nearly as well as freshly dried material. The preparation must first be wetted for a few seconds in ammonia (NH_4OH concentrated), then the ammonia must be completely removed with filter paper, and a large excess of Melzer's reagent must be added in order to compensate for any alkaline reaction still prevalent immediately around the fragment examined. Usually, a positive result can be seen without prolonged action of the iodine, yet if the result seems to be negative or inequal or doubtful at first, it is recommended to warm up the slide after about 20 minutes waiting, and then examine it.

The reaction is called amyloid or pseudoamyloid — if positive — and nonamyloid, if negative. The amyloid reaction is nearly black in some cases, in others it is a slight pallid grayish with a livid shade, with many intermediate shades between the two; pseudoamyloid (Singer, 1938) is a positive reaction if the final color obtained is brown to purplish brown. Nonamyloid walls are yellow to nearly

hyaline. Naturally, the reactions of strongly pigmented spores and hyphae, at least the strongly pigmented layers of their walls, cannot be inserted in this scheme since the reaction, one way or another, would be obscured, and covered up by the pigment, and treatment of these walls with substances that in the end would extract or destroy the pigment, would also alter the initial reaction of the wall. Consequently the question of amyloidity and therefore the use of Melzer's reagent is confined to hyaline or light colored (stramineous, palest melleous) tissues, and spores, and to the colorless endosporia of pigmented spores.

Amyloid reactions, obtained in the asci of the *Ascomycetes*, in the spore walls of the smooth spored *Leucopaxilli*, in the exosporial ornamentation of *Leucopaxillus* (Pl. XXIII A; 1 6), *Melanoleuca, Russula* (Pl. XIX, 2) and *Lactarius* (*Bondarzewia* among the polypores), and in the hyphae of the agarics are by no means equivalent to each other, or suggesting a similar chemical composition of these walls. Not only is the color obtained dissimilar (pure blue in the asci — pale livid gray to almost subhyaline in the smooth spored *Leucopaxilli* — blackish violet in the exosporial ornamentation - amethyst to deep red-brown, i. e. reaching a tone usually associated with pseudoamyloid reaction, in the hyphal walls) but solvents and dyes act in a different manner. Amyloid and pseudoamyloid reactions are clearly different in color in the spores of the *Basidiomycetes*, yet they intergrade almost unnoticeably in the hyphal walls. Amyloid reaction that is not of the amylon (starch) type becomes almost invariably pseudoamyloid in thick walled hyphal walls, and more amyloid in thin-walled hyphae or such hyphae where only a thin layer is iodine-positive. Locquin thinks that the exosporial ornamentation of the spores of the *Russulaceae* contains amylon which would almost certainly be true also for *Leucopaxillus* (warty spored species) and *Melanoleuca*. Another chemical composition is probable in other amyloid spore walls, and in pseudoamyloid walls.

Amyloid spores and hyphae were discovered at approximately the same time (1887) by Patouillard (*Aleurodiscus vitellinus*) and Rolland (*Mycena tenerrima*) in the *Basidiomycetes*, and in other fungi and lichens, amyloid reactions were known even before that. It was later found by Kühner (1938) that not only the hyphae of the stipe of *Mycena tenerrima* but all hyphae of the trama of most *Mycenae* are amyloid; he has later defined some sections in the genus *Marasmius*, and some of these sections, or parts of them, are characterized by

amyloid hyphae. More species with amyloid trama were found later by Singer (*Pseudobaeospora oligophylla*; *Poromycena anastomosans*, etc.). The author has also (1942) discovered epicuticular hairs that are somewhat intermediate between amyloid and pseudoamyloid, more frequently closer to the latter (*Crinipellis, Chaetocalathus*; *Lachnella, Merismodes*).

Kühner and Maire have first indicated a large number of Lepiotas with an unusual red brown reaction with Melzer's reagent which they interpreted as nonamyloid, but were later designated as pseudoamyloid by Singer, who also indicated that, aside from certain genera related to *Lepiota*, especially those with spores that have a germ pore, and the genus *Pseudobaeospora*, pseudoamyloid spores also occur in the genus *Chaetocalathus* (1942).

One species of *Marasmius* has cystidia which turn olive gray in Melzer's reagent.

All students of agarics will readily admit, after they have given the iodine tests a fair trial, that this microchemical method provides characters that are of enormous importance in taxonomy if evaluated critically, and used with discrimination. This may not always be the case in other groups of *Basidiomycetes* though it is certain that in the complex *Scutiger - Bondarzewia - Diacanthodes - Abortiporus*, in the group *Hericium* (and related *Corticiaceae*) - *Steccherinum* - *Dentinum*, etc., and also in the family *Leptotaceae* Maire emend. Sing. 1945, the amyloidity of the spores is very important — and in *Amyloporia* and *Amylocystis* among the polypores, the amyloidity of hyphae and cystidia also seems to have some taxonomic importance. In the agarics, this character must be used just as all other characters — cautiously, applying it as a specific character in the beginning stages of the investigation, and eventually — after enough data have become available — the amyloidity may or may not turn out to be a sectional (*Marasmius, Cystoderma*), a subgeneric (*Amanita*), generic (*Mycena, Pseudohygrophorus*), tribal (*Panelleae*), or even family character (*Russulaceae*). The same is true for pseudoamyloidity (generic character in *Lepiota* and all *Leucocoprineae*, *Crinipellis* and allied genera). There can be no methodical determination of agarics without Melzer's reagent and a careful study of its action upon the walls of the spores, hyphae and epicuticular elements. As has been said before, it may well be that the term «amyloid» should be supplemented with a few more terms, indicating more clearly the quantitative and qualitative composition of the mixture of amylaceous

and « amyloid » substances that make up the walls of the fungi. A first step in this direction is perhaps the introduction of the term pseudoamyloid which — without a chemical analysis — is based on a difference in color. Perhaps, the reaction of the exosporial ornamentation of certain white-spored groups, in the first place the *Russulaceae*, should be described as amylaceous rather than amyloid. It is felt, however, that a hasty introduction of new words for chemically and physicochemically unknown or halfknown phenomena is premature unless the optical effect is different enough to warrant such a distinction. It is also hoped that the examination of the amyloid substances in the fungi will become clearer in detail when each iodine stain is accompanied by a series of other microchemical reactions and metachromatic colorations with a large variety of dyes. The positive and negative result for every single one of these will then serve as a further modification of the amyloidity as it is now understood in a very general way.

It was Josserand's (1942) idea to remove the amyloid exosporial ornamentation with certain organic or inorganic solvents of amylaceous and amyloid substances or mixtures containing such. Locquin was more methodical about this (1943); the author refers to Locquin's paper on the subject because it appears that this method may have some influence on a future subdivision of the amyloid reactions on one hand, and on the introduction of the fundamental ornamentation in taxonomic mycology on the other.

Locquin, for this purpose, used nitric acid, zinc chloride (solvents of starch containing spore walls), ammonium oxalate (for walls containing pectine compounds), NaOH and KOH (for walls containing hemicelluloses), and sodium hypochlorite (for chitin). Some of these reagents are also used in other micro and macroscopical tests newly introduced into taxonomic mycology, especially in the *Agaricales* (but also in the *Aphyllophorales*, and with a great potential importance in the *Gastromycetes*, and perhaps the *Ascomycetes*). We shall first review the microchemical tests:

Potassium hydroxyde, KOH (which can be substituted by sodium hydroxyde, NaOH), is used in *Cystoderma* (Smith & Singer, 1945) since it darkens certain layers of the covering of the pileus in certain species whereas this reaction is not noted in others. It has been found a valuable additional character. In fact, the main classification of the genus, in the new monograph, is rightly based on two microchemical characters, amyloidity and KOH reaction. In *Crinipellis mira-*

bilis, the epicuticular hairs become gray in KOH (Singer, 1942). KOH also causes a green discoloration of the carbonaceous articles in the trama of *Anthracophyllum* (Singer, 1944). In concentrated H_2SO_4, the spores of certain *Coprinaceae* change from black to pale livid whereas in others the same black or fuscous membranal pigment is resistent (Kühner, 1929); this reaction has been used for the classification of the *Coprinaceae* by Singer (1936). Another taxonomically important reaction was that obtained with ammonia (NH_4OH) on the internal body of the cystidia of *Stropharia, Naematoloma, Pholiota* (Kühner, 1936); these cystidia were later distinguished from other (pleuro)cystidia of the *Strophariaceae* and the *Agaricales* as a whole by Romagnesi, under the name chrysocystidia (Pl. XVII, 3). The author has found deep blue contents in cresyl blue mounts, and therefore thinks that the chrysocystidia are chemically — if not otherwise — related with the gloeocystidia. The trama of *Xeromphalina caulicinalis* and closely related forms turns red with ammonia (NH_4OH) according to Singer (1936); this reaction is due to a transformation of the brown, incrusting pigment of the hymenophoral trama. Another group of species in this small genus, does not show this reaction. Kühner (1935) has first noticed and used as a character in his *Galera* monograph, the needle-like crystals that are formed in preparation of the hymenium in various species of *Conocybe* whereas other species of the same genus do not form them. Singer (1937) reported the same long, colorless needles in ammonia preparations of the hymenophore of *Phaeomarasmius Wuestandri*. This is the first chemical micro reaction that is not a color reaction.

Several other microchemical characters have since then been added to the above, viz. the reddish pigment in the *Gomphidii* that shows in a formaldehyde acid solution, and other characters based mainly on the solubility of fungus pigments (see. p. 105). The widest application of microchemical reactions is now made in the *Russulaceae* where a mixture of aldehydes with strong acids is known to provoke a darkening of the contents of the macrocystidia, dermatopseudocystidia, and some oleiferous hyphae and laticiferous vessels. The reagents used are:

Sulfovanillin:

Chemically pure vanillin........	0.5 gr
Distilled water........	2.0 »
Pure sulphuric acid........	4.0 »
Sulfovanillin........	6.5 gr

The resulting solution is of a deep rich yellow. It should be filtered through glass wool, or handled very carefully as the unsolved crystals and those that form after a while when the solution begins to disintegrate, often cover the section studied, and, under pressure, the cover glass may easily be broken. Sulfovanillin must be used on fresh material. It is true that the results are sometimes satisfactory with well dried material during a period of several months after collecting but they are no more conclusive if the reaction is negative.

Sulfoformol :

Formaldehyde 40 p. c. watery solution..........	6 ccm
Distilled water........	3 »
Pure sulphuric acid........	10 »
Sulfoformol..................................	19 ccm

The resulting solution is colorless. It must be used on fresh material or on material that has been in formalin for not more than 6 months.

Sulfobenzaldehyde :

Same as sulfoformol, the formalin replaced by benzaldehyde.

Chlorovanillin :

Same as sulfovanillin, but the sulphuric acid is replaced by concentrated hydrochloric acid.

All four reagents give parallel reactions :

Organs of the *Agaricaceae*	Sulfovanillin	Sulfoformol	Sulfobenzaldehyde (or sulfoparadimethyl-aminobenzaldehyde)	Chlorovanillin
Macrocystidia, Dermatopseudocystidia, some oleiferous and laticiferous vessels.	blue	brown	black	blue
Cystidia, gloeocystidia, basidia, hyphae, ciliate dermatocystidia, primordial hyphae	hyaline to rose color	hyaline	hyaline	hyaline to rose color

Sulfoformol has also been tested in the pseudocystidia of *Lentinellus* where it gives the same results as in *Russula* and *Lactarius*. All these reactions have been used on a large scale by R. Maire (since 1907). Sulfovanillin was introduced into lichenology by Lindt (1885), and in mycology by Arnould & Goris (1907). They are now generally used in *Russula*, *Lactarius*, and *Lentinellus*.

Macrochemical color reactions

Macrochemical color reactions were first used for the determination of certain polypores. Muller (1872) discovered the violet discoloration taking place when *Hapalopilus nidulans* is exposed to ammoniac vapors. Harlay (1896) discovered the deep violet discoloration of the pigment of *Lactarius necator* with alkali which can be used as an indicator — in acid solutions, the same substance turns pale pink. This reaction is unique among the *Lactarii*, only *L. necator* and, according to the experience of the author, *L. atroviridis* show it. In the same year, Bourquelot & Bertrand introduced guaiac, whose reaction with fungous tissues had been discovered by Schonbein (1856), into general use in the *Agaricales*, and in 1907 Arnould & Goris initiated the use of sulfovanillin in *Russula*. Since then, some authors continued to study the action of chemical reagents on the various parts of *Basidiomycetes*, especially agarics (Bataille, R. Maire, Barlot, Kühner). But reagents did not become routine tests in any group of *Agaricales* until Melzer & Zvara (1927) introduced a whole series of chemical reactions, and, at the same time used the reactions for taxonomic purposes; in fact, the subdivision of *Russula* in Melzer & Zvara's monograph is almost too much based on chemical reactions. In 1938, J. Schaeffer & Moller introduced the use of several chemical characters in the taxonomy of the genus *Agaricus*, and in the same year, chemical characters were first used in the *Boletaceae* and *Gomphidiaceae* by Singer, and new reagents were added to those already used in *Russula* and *Lactarius* by Heim. Also in 1938, the first general survey of the reaction of guaiacol was made by Singer, and it was shown that even in *Russula*, the genus for which it was first introduced, the reactions are constant in some species, and inconstant and unreliable in others. At the same time, the author used chemical characters for the delimitation of genera, and in phylogenetic problems, and so did other authors (Heim, Romagnesi). In 1939, Boasset recommended the use of monomethylparamidophenol for chemical tests of

Basidiomycetes, and his findings were supplemented by numerous tests of this particular reagent in the author's papers, and he as well as other authors widened the scope of application of Melzer & Zvara's reagents beyond the genus *Russula*. Especially $FeSO_4$ and Fe_2Cl_6, phenol and formaldehyde have become standard reagents for the laboratory and even for extended field trips. Henry makes use of these and other chemicals in his work on *Cortinarius;* Singer on *Paxillus;* Konrad & Josserand on *Collybia*, etc.

This is in short the history of the macrochemical color reactions up to the war. The tendency to use these characters has rather increased than decreased since then.

The following is a list of the most important chemical reagents, the reactions obtained and the genera in which they are used most frequently:

1. *Reagents of oxidases*

Guaiac. Ordinary guaiac tincture: the oxydases present in fungi act on the guaiaconic acid present in the resin, if atmospheric oxygen is present. A blue (or green) to purple spot is formed at the surface of the section through the stipe in all those agarics and boletes that react positively. The reaction can be used in all genera. The time necessary to obtain the first result should be noted. Indispensable in *Inocybe*.

Guaiacol, watery solution, slightly below the saturation point. Reaction, if positive, from salmon color orange to rose color or bluish pink, slowly darkening to dark copper or chocolate color in most cases; the base of the stipe is always most sensitive; the reaction is useful in the *Russulaceae, Tricholomataceae, Amanitaceae*.

Pyramidon in saturated, watery solution. In species with positive reaction, the context of the stipe becomes light lilac color. It is used only in *Russula* and *Tricholoma*.

2. *Other organic reagents:*

Phenol (carbolic acid), 2 p. c. watery solution; reaction either negative or positive; if positive, it is chocolate color, or deep purplish violet after 20 minutes; in some cases the reaction is more sordid grayish vinaceous, reddish, etc. If after 20 minutes no distinct reaction has taken place, the reaction is called negative, even though it may show up after an hour (Amanitas of the phalloides group). Indispensable in *Russula* especially the mild tasting species. *Amanita*, especially the exannulate and the amyloid spored groups, in *Leccinum*, also used in the *Tricholomataceae* generally, and in *Lactarius*.

Formaldehyde (formalin, formol), 40 p. c. watery solution; reaction varies; it usually is positive in such species that have a tendency to change the color of the context by autoxydation, yet, at times it may act in the opposite way, inhibiting the autoxydation. This is also a slow reaction, and sections treated with formaldehyde should be observed at least 20 minutes. This reaction is indispensable in *Russula*, *Tricholoma* (the clampless group), *Gomphidius*, *Leccinum* and other boletes.

Aniline (aniline oil and aniline water). This is either pure aniline oil, or the «oil» mixed with an equal volume of distilled water. Since 1932, aniline oil is used almost exclusively. It becomes red to copper red on wounds of the stipe of mature *Russula xerampelina* and allied species, and is more or less parallel in its reaction with that of ferric sulfate. It is also specific in certain cases with the lamellae of the *Russulaceae* where it causes a central stained spot and then a characteristic gray or bright colored zone around it (especially important for *R. emetica*). Also occasionally used in other groups, e. g. boletes, *Agaricus*, and, among aphyllophoraceous genera, *Scutiger ovinus*. In *Russulaceae*, especially on the lamellae, the reaction is slow.

Cross reaction. This was described by J. Schaffer and Moller, and consists in a test made on the surface of the pileus of the species of *Agaricus* whereby a transversal streak with HNO_3 is made, and then crosswise, another streak with aniline oil. The result, if positive is an orange red to fire red discoloration. It must be considered, however, that the two substances often react with each other without interference of the *Agaricus* whereby a colored crystallized mass is formed that may be misleading.

Phenol aniline. This consists in the mixture of a few drops of aniline in phenol (2 p. c. watery solution). While all the preceding reactions have to be performed with fresh material, never with dried or otherwise prepared material, this reaction is recommended by J. Schaffer for dried material of *Russula*. The reaction is from nil to nearly black after prolonged exposure.

Sulfovanillin, sulfoformol, sulfobenzaldehyde and chlorovanillin. The formulas are the same as those given under microchemical reactions. For macrochemical color reactions, the first and the last of these reagents are preferred. They are used mainly for the identification of certain *Russulae* (*R. rosea*, *R. minutula*, *R. albida*, etc.) in which the context of the stipe and, especially, the surface of the stipe, with sulfovanillin immediately turn very bright red, and

remain that color (Pl. 1, L 6, becoming Pl. 2, L 6, then Pl. 3, L 6, finally Pl. 4, L 6); any stain less bright red, such as « Tommy red », « Red Cross », or even more purple or carmine, or tending to brown or blue, and soon disappearing or becoming very deep colored, is considered as negative. With chlorovanillin, the difference between positive and negative is even more conspicuous (the negative reaction being not deeper than « baby rose », « candy pink », « coral », « confetti »). The reaction with *R. albida* is not quite as striking as that with the two red species. All color indications are in Maerz & Paul terms. Sulfovanillin has also been used by Kallenbach and Romagnesi for *Boletaceae* but its use in that family is hardly justified since the reactions are those of sulphuric acid. Sulfoformol is used for these same *Russulae*, that turn red with vanillin, and also, according to Bataille, with *R. luteotacta*, *R. rosacea*, *R. Queletii*, and according to Singer, with *R. subalbidula*.

Alpha-naphthol. A scalpel tip full of the reagent is dissolved in about 2 ccm of 90 p. c. alcohol, and then 4 ccm water are added. The solution reacts almost uniformly with the context of the stipe of *Russula* causing a deep indigo to violet blue discoloration after a few minutes. Some species react very slow, or perhaps not at all. It would be interesting to know what results — if any — can be obtained in other genera.

Pyrogallol. A 5 p. c. watery solution is said to give richly colored (yellow to brownish yellow) reactions with the context of the *Russulae*.

Monomethylparamidophenol (« methol »). The crystalized reagent, often used in photography, is dissolved in about 20 times its weight of distilled water, the solution is used immediately since it is unstable. The positive reaction varies from a pale sordid lilac or lilac (« vinaceous purple » of Ridgway, or more sordid), finally reaching « dark nigrosin violet », « deep naphthalene violet », « blackish purple », « taupe brown », etc. The reaction sometimes passes through pink or salmon, and sometimes through blue (*Lactarius volemus*), and at times becomes arrested at these colors. In other cases a more yellow reaction is observed which is probably of another chemical nature than the violet one which is obviously due to the fact that the fungus tissue contains some substance that yields oxygene to the reagent. The same capacity as reducer may also prevent the autoxidation that takes place in the bluing *Boletaceae* when monomethylparamidophenol is added before the discoloration of the context starts.

The negative reaction is neither preventing any natural discolorations, nor does it show any pink, salmon, blue, violet, or yellow discoloration provoked by the reagent itself, and the darkening that is often seen after a very long time is rather due to a transformation of a different order than to the reaction called «positive» here. The reaction is variable with a large number of species, but with others it is quite constant, and a variable amount of time (1 — 30 minutes) is required to reach the different stages of the reaction. This difference in time is perhaps more important than the differences in shade which do not seem to be very constant. The reagent must be applied on fresh, mature, not watersoaked material. It gives good results in many groups, almost uniformly — as far as limited experiences allow to state — in *Russulaceae* (weak reaction in *Russula fellea*) and *Lyophylleae*. It is, generally speaking, more valuable in white spored agarics than in dark spored groups and in the boletes.

Methylchlorantimoniate (in methylalcohol solution) is a reaction designed to translate the acrid taste of the *Russulaceae* into an optical character. The positive reaction is lead gray, the negative reaction is unchanging (or belatedly becoming slightly bluish context.

Ethylchlorostannate (alcoholic solution) is said to give a yellow brown reaction with *Amanita gemmata* (under the cuticle) whereas all other species examined in this genus are completely negative.

3. *Iron salts.*

$FeSO_4$, Fe_2Cl_6, and ferric alum can all be used for the same purpose, the first of them being the most commonly used, in 10 p. c. watery solution, on fresh mature specimens. The discolorations are of several categories (1) none, i. e. negative reaction — no color change, or color change indistinct; (2) some kind of olive, green, blue green, blackish green discoloration of the context of the stipe — often also the surfaces; this reaction is widely distributed in agarics and boletes, especially in *Russula xerampelina* and related species, *Lactarius volemus* and related species, some *Russulae*, *Compactae*, some species of *Tricholoma* and *Tricholomopsis*, many *Cortinarii* and other dark spored agarics, many *Boletaceae*, *Gomphidius*, etc. In the genus *Gomphidius*, the reagent differentiates the presence of a chemically distinct subhypodermial layer. (3) All gradations from a rather pure pink or salmon color to sordid gray with or without a slight mixture of reddish. This is the ordinary reaction with the *Russulaceae*, with *Tricholoma albobrunneum*, and other agarics. (4) Blue or green blue to slate gray. This reaction is commonly found in *Leccinum* where the

gradation between blue and gray is of taxonomic importance; also in other boletes. (5) A variable color effect on the cuticle of the pileus (e. gr. *Russula ferrotincta*).

4. *Ammoniac* :

Ammoniac vapors (NH_3) and ammonium hydroxyde, concentrated solution (NH_4OH), are both used. They must be used on strictly fresh specimens, on all organs separately. The color effects are very varied, and often differ in different organs as well as with the age of the carpophore and temperature (specimens that had been exposed to freezing temperatures sometimes react differently). The most valuable results were obtained in the *Strobilomycetaceae*, *Boletaceae*, *Gomphidiaceae*, *Paxillaceae*, *Cortinariaceae*, and *Agaricaceae*, but also with some genera of the *Tricholomataceae*, with *Russula* and *Lactarius*.

5. *Strong alkalis* :

Potassium hydroxide (KOH), 15 p. c. solution in water (some use 10 p. c.), and sodium hydroxide (NaOH), same concentration, act in the same way in all cases known to the author. KOH is a standard reagent for all groups of *Agaricales* used in fresh and in dried specimens separately, on all organs separately. The action can often be reverted at a given pH by application of a diluted acid, and certain pigments of *Agaricales* (*Lactarius turpis*, *L. atroviridis*, *Collybia iocephala*) are good indicators. KOH as a reagent, specific for certain species or groups of species, is indispensable in the *Strobilomycetaceae*, *Boletaceae*, *Agaricus*, *Amanita*, *Leucoagaricus*, and *Cortinarius*. The action is almost instantaneous.

6. *Strong acids* :

Sulphuric acid (H_2SO_4), concentrated. Used on fresh specimens of *Amanita*, also on boletes, some *Tricholomataceae*, *Gomphidius*, *Cortinarius*, *Agaricus*, *Lepiota*, *Leucoagaricus*, etc. Less important than KOH, this reagent must be used on fresh specimens. The action is instantaneous or almost so.

Hydrochloric acid (HCl), concentrated, used as above.

Nitric acid (HNO_3), concentrated, used as above.

Those who go beyond the verification of data already available, by testing thus far untested species, or species whose reactions have not yet been published, will do well to adhere closely and consistently to the formulas, and also to constant and equal conditions and methods. It is also extremely important to avoid painstakingly interference between different reagents. Phenol and anilin can never be used on the same carpophore, and without utmost cleanliness.

Ammoniac vapors should be kept from other reagents, especially $FeSO_4$. Young specimens should not be taken into consideration, or only for the sake of comparison with adult specimens. Generalizations should be made only after a long experience with the species in various ecological conditions, and with the behavior of the reagent under various chemical influences. The colors obtained should be indicated in color chart terms wherever this appears to be advantageous.

Chemical analysis of the carpophores

The use of chemical analysis of the carpophores of the *Agaricales* is merely in the beginning stages as far as their taxonomic value is concerned. However, some of the possibilities will be mentioned here because even the fragmentary data now available show that results of taxonomic importance might well be expected.

In this category belong the demonstration of the formation of cyanic acid by certain agarics. In order to become more conclusive, the list of agarics known to produce HCN beyond a certain minimum amount (according to the sensitivity of the picric acid method), should be supplemented with a list of the species that under these circumstances do not show any appreciable formation of HCN. More than half of the species indicated by various French authors [1] have

[1] The last complete list published is that of Josserand (*Rev. Myc.* 3 : 29, 1938). Several more species were indicated later :

Cantharellula obbata, C. cyathiformis ;
Clitocybe Alexandri, C. fragrans, C. infundibuliformis, C. parilis, C. geotropa ;
Collybia dryophila ;
Lepista nuda (this has not been verified by other authors) ;
Pleurocybella porrigens ;
Leucopaxillus giganteus ;
Marasmius globularis, M. oreades ;
Rozites caperata

The tests have been made with the picric acid method which consists of the following procedure. The specimens are, in strictly fresh condition, cut into fragments, and inserted in a glass vessel that can be closed nearly airtight (exsiccator). A piece of filter paper (2 x 20 cm) is immerged in a solution of picric acid (1 p. c.). After the paper has dried the same paper is immerged in a 5-10 p. c. solution of sodium carbonate (repeat this operation several times, leaving the paper in the $NaCO_3$ solution several seconds each time). The paper is then hung riding on the rim, and the vessel closed firmly. The paper outside remains yellow ; the paper inside becomes slowly (over night) dull red if the fungus exhalates HCN

been checked by this author on material from the United States, and the result was positive in every case. This points to a strong specific constancy of this character, and the comparative simplicity of the method of qualitative demonstration of cyanic acid in agarics makes it possible to use it more extensively than is done at present.

Quantitative analyses of certain specific carbohydrates, acids, etc. are also useful in taxonomy though they cannot be expected to become routine tests for determination. For instance, Heim & Romagnesi (1934) referred to the analyses that were made on a rather large (yet still insufficient) number of *Agaricales* in regard to allantoic acid. Heim & Romagnesi found that the high percentage of this acid present in *Coprinus* and *Leucocoprinus*, as against a low percentage in *Macrolepiota*, shows a certain chemical affinity between *Coprinus* and *Leucocoprinus* and increases the hiatus between *Leucocoprinus* and *Macrolepiota* on the other hand. These data are based on a paper by Fosse & Brunel (1933).

Frerejacque (1939) published a list of species which he had studied as to their contents in mannitol. He states that the list is not complete enough to make final conclusions. But it is obvious that the figures representing the weight of mannitol per 100 gr of the dried carpophores, keep in definite limits characteristic for certain groups of fungi. So we find a medium to high percentage of mannitol in *Gomphidius* (which is thus chemically separated from the other black spored agarics), *Paxillus*, and boletes; in the natural group of *Lactarius* and *Russula*, he indicates a medium to usually high percentage of mannitol, with *Russula delica* showing a more than twice as high percentage than *Lactarius vellereus*. There is also a rather high percentage in *Agaricus* and *Leucoagaricus* whereas in *Lepiota* it is abruptly very low. This would tend to show chemical affinity between the *Agaricaceae* with germ pore; in the *Tricholomataceae*, the figures are low to rather high (up to 10.0 in *Armillariella mellea*), and in all other groups consistently low (to zero in *Inocybe maculata*).

A large number of facts, many of them concerning the *Agaricales*, have been assembled on the coloring matter in fungi by I. A. Pastac (1942) but this interesting survey that is recommended to those concerned with fungus chemistry, shows clearly enough that the accumulation of facts has not arrived at a level where data of taxonomic value can be derived with safety. Especially promising aspects are the data available on atrotomentine, boletol, dermocybin, muscarine and others.

XIV. PHYSICAL CHARACTERS

It has been suggested (but never realized in experiments) to compare the specific weight of dried carpophores and make tests on their elasticity. These tests are almost impossible to translate from speculation into reality. The specimens vary too much in different ages and under different climatic conditions, habitat conditions, and by intraspecific variation — as every mushroom grower will readily confirm. Another approach is that of provocation of luminescence by application of polarized light and Wood's light on various fungi, and the conclusions are though neither too encouraging nor too disillusioning, in any event worth the attention of the taxonomist. Josserand and Netien think they have found another difference between *Russula* and *Lactarius* in the behavior of the carpophores in Wood's light, and this recalls a similar attempt, still unpublished, I believe, by Zuderell, Cernohorsky and Singer, with polarized light, where the most striking effects of luminescence were obtained with *Russula*, whereas the *Lactarii* remained almost dead. For more detailed evaluation of these results the reader is referred to the authors of the paper cited above (*Bull. mens. Soc. Linn.*, Lyon, reprint, p. 1-20).

XV. CYTOLOGICAL CHARACTERS

Nuclear cytology

Cytology in the wider sense is now frequently applied in the taxonomy of the *Agaricales*: it has even found its way into the basic keys for determination in monographs as well as in surveys of genera.

The number of chromosomes has not yet been used by systematists; it seems to be generally rather low, and differences in shape apparently do not exist, or have not been brought to the attention of the mycologists.

The nuclei, as a rule, are small to very small, and their number in the mycelium, the hyphae of the carpophore, cystidia, basidia, and spores differs according to races, species, or larger groups of species or genera. This whole problem cannot be studied without due consideration of the whole life cycle and sexuality of the *Agaricales* whereby certain types and aberrations from the normal form will

be considered separately, with their taxonomic application in view.

The most important contributions were made by Maire (1900-1902) and later Kühner (1926-1945). Many other authors have contributed important details without, however, attempting to evaluate them for taxonomic purposes.

Summing up what is generally considered as the « normal » life cycle of an agaric and bolete, we shall start with a uninuclear spore that after germination gives rise to a haploid (monocaryotic) mycelium (also called primary mycelium, a term that should be abandoned). The septa between the hyphae of the haploid mycelia are clampless (except for a very few reported cases of « autodiploidization »).

The spores as well as the haploid mycelia resulting from them are all morphologically different, therefore the « normal » type of *Agaricales* comes under the group of so-called heterothallic thallophyta. Heterothallism in fungi was discovered by Blakeslee (1908) and in the *Agaricales* by Bensaude (1918). The sexuality of the heterothallic *Agaricales* appears in two forms, one of which is called bipolarity, and represents the usual bipolar isogamy among the representatives of this group, and another that was discovered by Kniep (1922) in which the mycelial descendants of a carpophore are physiologically divided in four instead of two groups, according to the schema :

	M1	M2	M3	M4
M1 .	—	+		
M2 .	+	—		
M3	—	—	—	+
M4	—	—	+	

This means that in the bipolar forms, of the two physiologically different types of mycelium, each can copulate with the other type, whereas in the tetrapolar type, a mycelium of the type 1 can copulate only with a mycelium of the type 2, and a mycelium of the type 3 can copulate only with a mycelium of the type 4. In other words, we have here a form of sexuality with four sexes instead of two, a fact that made it necessary to emend the conception of sexuality (this is Quintanilha's opinion - but compare H. S. Jackson, *Trans. R. Soc. Canada* **38** : 4 5, 1944).

The study of the copulations is technically achieved by single spore cultures [41].

[41] As for methods we refer to special papers, especially by Vandendries.

After the copulation of two mycelia of the haploid generation, the second generation, normally the more important one in the *Basidiomycetes* (because the carpophores are usually produced by it), begins with the formation of the dicaryotic (sometimes called secondary) mycelium, or the mycelial phase of the dicaryophyte. The dicaryophyte immediately starts the formation of clamp connections and the cells consistently contain two nuclei which divide at the same time and pass into the new cell in a rather complicated way that is reminiscent of (and according to most contemporaneous authors homologous with) the similar hook formation of the ascogeneous hyphae (*Ascomycetes*). One nucleus of the pair resulting from the division of one nucleus of the original dicaryon enters a bulge that points outwards and backwards at the place where the new septum will be formed. The bulge — called clamp now — fuses with the parent cell, the double wall becoming dissolved, and the nucleus that was in the bulge enters the parent cell. At the same time, between the two nuclei of the second pair resulting from the division of the second nucleus of the original dicaryon, a new septum is formed inside the old hyphal cell, separating the new cell from the old one and thus leaving one nucleus of each pair in each cell. The two in the old portion and two in the new cell are now separated from the clamp by the laying down of an additional septum. The resulting structure, characteristic for the *Basidiomycetes*, is called a clamp connection (Pl. XI, 3; XXIII A, 7). These clamp connections are normally present on all or almost all hyphae of the whole dicaryophyte, including the carpophore. The dicaryotic mycelium contains two nuclei in each cell because, after the fusion of two haploid mycelia with opposite polarity, the nuclei — though entering the same hyphae and remaining in pairs all through the dicaryophytephase — do not fuse to form a diploid single nucleus. Thus reduction division is postponed throughout this generation and finally takes place in the basidia of the carpophore [43]. Normally, only the dicaryotic mycelium is able to form carpophores. The hyphae of the carpophore and also the basidiole are typically binucleate (Dangeard, 1895). The reduction division is usually followed by one or two more divisions which take place in the upper part (club) of the basidium, and the spindles of the first two, or at least the second division are in an obliquely subhorizontal or in an almost horizontal

[43] Falck (1902) calls the carpophore phase of the dicaryophyte « tertiary mycelium, an unnecessary and misleading term that must be abandoned

position, the spindles of the second division often forming an X shaped (chiastic) figure. This is in contrast to the stichobasidial type in which the figures of this division are found one beneath the other in a more nearly vertical position and at a lower level of the basidium. There are probably what may be termed as transitions between the basic types — chiasto — and stichobasidia — but not normally on the level of the *Agaricales*, nor, for that matter in the holobasidial *Aphyllophorales* (excluding the *Exobasidiales*), where both types occur in otherwise rather closely related forms such as the *Clavariaceae* sensu lato and the *Cantharellaceae* sensu lato, and in the *Gastromycetes* where only chiastic basidia are known. After the second division, there will be four nuclei in the basidium, and in the simplest case, these four nuclei ascend to the sterigmata which by this time have been formed, and the sterigmata bulge out at their apices where the uni nucleate spore is formed. This completes the life cycle of a « normal » representative of the *Agaricales*.

This life cycle can, consequently, be expressed by the following scheme :

1. *Bipolar species :*

Basidiospore + → haploid mycelium + → } dicaryotic mycelium →
Basidiospore — → haploid mycelium — → }

→ Carpophore → binucleate basidiole → Basidium { o o o o } four basidiospores

2 [41] *Tetrapolar species* (Aa, Ab, Ba, ab, AB . pairs of Mendelian factors)

Basidiospore Ab → haploid mycelium Ab → { dicaryotic mycelium → carpo-
Basidiospore Ba → haploid mycelium Ba → } phore Ab . Ba →

→ Binucleate basidiole { o o basidiospore AB or AB or Ab
Ab . Ba — Basidium { o basidiospore ab or ab or Ba
o basidiospore Ab or AB or Ab
o basidiospore Ba or ab or Ba

For taxonomic purposes, only the aberrations from this scheme are of interest, and as far as they present constant features, they can be used.

[41] See QUINTANILHA, A., *Le Problème de la Sexualité chez les Champignons* — *Bol. Soc. Brot.* 8 (11), 1933.

As for techniques of cytological investigations in the *Agaricales*, we cannot go into detail. However, it is recommended to start with an organism which is easy to collect in all stages, easy to fix and dye and uncomplicated in its development. Such a species is, for example, *Collybia dryophila*. It is advantageous to carry the fixative on collecting trips and insert the fragments, properly labeled, right in the field. Every genus, and every tissue, the mycelium, the basidium, and the spores, require an individual treatment as far as fixation and coloration are concerned, and there is no never failing method that works with all cells of all fungi. However, Kühner (1938, 1945) has published repeatedly on the subject, and the chapter on cytology in his *Mycena*-monograph as well as a later article on the study of the distribution of the nuclei in the mycelia of the *Basidiomycetes* is recommended.

In 1934, Chow stated that in certain *Coprini* the mature spores are binucleate, in 1933 Kühner reported the spores of *Marasmius rotula* uninucleate. Later (1945) he indicates that in the *Amanitaceae*, *Bolbitiaceae*, *Cortinariaceae*, *Strophariaceae*, and most *Agaricaceae*, the spores are binucleate at the moment of discharge and afterwards. This is explained by the fact that the third division of the nuclei after meiosis (comparable with the third division of the asci of the *Ascomycetes*, resulting in eight uninucleate ascospores) usually takes place in the spores rather than in the sterigmata or basidia and must result in binucleate spores. In most *Hygrophoraceae* and most *Tricholomataceae*, however, the third division takes place in the sterigma and only one nucleus ascends to the spore while the other descends back to the basidium where it degenerates. Thus, only one nucleus is present in the spore at discharge and immediately afterwards; however, the author has found this single nucleus dividing later on while still in the spore, and consequently some of the spores are then found to be binucleate and some uninucleate. The number of nuclei in the spore is easy to establish, and has undoubtedly a great taxonomic importance.

The bi- and tetrapolar forms, the germ tube and the whole initial stage of the mycelium is usually multinucleate and later becomes septate and uninucleate until copulation, whether it starts from a binucleate or a uninucleate spore. It is known, however, that in many cases, the mycelium resulting from germination of the spores is immediately binucleate, i. e. the haploid phase is not at all represented, and the life cycle of these species starts out with the dica-

ryotic mycelium. These forms are called homothallic (Blakeslee, 1904) because the thallus does not show any change of generations. Homothallism is obviously a characteristic of the genus in *Clitopilus* (Kühner & Vandendries, 1937). Many species are known in which homothallism is either the rule, or is found in special races of the main « normal » form. The latter case is frequent in such groups where 2-spored forms and 4 spored forms are known in a species (such as *Mycena*, *Mycenella*, *Marasmiellus*, *Conocybe*, etc.) whereby the 4-spored form usually represents the normal form, and the bisporous form the homothallic form. Clamp connections are sometimes absent in homothallic forms but, of course, not necessarily so.

The life cycle of homothallic dicaryophytes can be shortly described as follows:

1. *Bisporous form:*

Binucleate basidiospore — dicaryotic mycelium — dicaryotic carpophore —

binucleate basidiole — basidium — two binucleate basidiospores

2. *Tetrasporous form:*

Binucleate basidiospore — dicaryotic mycelium — dicaryotic carpophore —

binucleate basidiole — basidium — four binucleate basidiospores

In other forms, the haploid mycelium is able te form carpophores without previously forming a dicaryotic mycelium, i. e. every single spore (as in the homothallic dicaryotic forms) is apt, theoretically, to form carpophores and another generation of spores without interference of another mycelium. In spite of the fact that these carpophores are necessarily composed of uninucleate hyphae, and there is no reduction in the basidium, the formality of the formation of uninucleate basidioles is nevertheless conserved. The single basidial nucleus divides as in any other cell, and the resulting two nuclei move into the spores, one into each of the two spores. This is the case, for example in *Mycena galericulata* forma *bispora*, and the fructification

is then called parthenogenetic. Parthenogenetic carpophores, naturally, never have clamp connections [44].

The parthenogenetic forms are, as far as we know, not characteristic for larger taxonomic groups but merely for certain hereditary races, with « normal » and sometimes dicaryotic-homothallic parallel races. Consequently, the number of sterigmata on the basidia is not necessarily the expression of a certain type of life cycle, i. e. it is impossible to say whether it belongs to a dicaryotic-homothallic or a parthenogenetic form unless the nuclear divisions are carefully studied from the basidiole to the spore. It is probable, and, in the author's opinion, logical to expect that some of the normal (bipolar or tetrapolar) forms have died out, and the bisporous homothallic-dicaryotic or parthenogenetic form alone has survived. Such seems to be the case, according to all taxonomic evidence, in certain species of *Laccaria*, and, if so, these species posses bisporous basidia as a specific character. Though, on the basis of the data available, it must be assumed, that these bisporous *Laccariae* actually are species, this represents the exception rather than the rule, and we can now say that Lange (1914) overestimated the importance of the number of the sterigmata. Besides, the situation is not always as clear-cut as it may appear on a scheme. In many specimens with basidia developing sterigmata of a number lower than 4, the 2-spored basidia are inter-

[44] Even if the absence of clamp connections in the carpophore and the presence of but one nucleus in the hyphae can be demonstrated, the specimen studied is not a priori parthenogenetic, for one of the following two reasons:

1. It may be that the sole nucleus is diploid whereby the fusion takes place immediately after copulation of the hyphae which may have been overlooked, or without any copulation, whereby the species would be homothallic-diploid. This explanation is contrary to all we know in the *Agaricales*, and, aside from that, highly improbable since parallel races of wholly uninucleate forms are binucleate and bipolar or tetrapolar in the manner described as « normal ».

2. It may also be that the sole nucleus is haploid until, by now unknown means, the basidioles become binucleate, yet the four spores are again uninucleate. Here we have a life cycle in which the dicaryotic phase is shortened to the limit — something similar to the correspondent phase in the *Ascomycetes*. Yet, this type of sexuality, the so-called *Typhula* type, has been observed in *Agaricales* only once (Chow, 1934, in *Coprinus fimetarius*), and it remains to be seen whether this latter observation is correct, and if so, how common it is under normal conditions of culture and in the field. It is probably at most a rare exception in the *Agaricales*.

This shows, that theoretically at least, in all cases, a complete cytological study is needed in order to arrive at exact results.

mixed with 1-, 3-, and 4-spored basidia which usually results in a marked polymorphism of the spores which vary between widely separated extremes of length and breadth, the volume of the spores from 1-, 2-, and 3-spored basidia decreasing (in this order), and the 4-spored basidia developing the smallest spores. These facts can be explained by cytological irregularities — very frequent in fungi — which do not interest us here since their taxonomic value is close to nil.

The absence of clamp connections (Pl. XXIV; XXVII) can also by no means be linked with parthenogenesis exclusively. Clamps are often absent on the septa of binucleate hyphae, and there are rare, thus far not fully explained cases where clamps have been observed on the haploid mycelium. For taxonomic purposes, we may neglect the latter case, but if the presence or absence of clamp connections is used as a character in taxonomy, it is essential to make sure that the specimen studied is not merely a parthenogenetic form of a normally bipolar or tetrapolar species. If this possibility is excluded, we have further to deal only with species with normal sexuality that have lost their ability to form clamp connections, and homothallic forms, species, or genera, that find themselves in the same condition. Under these circumstances, the presence and absence of clamp connections must be accepted as a valuable character. Vandendries was the first to emphasize that a defined species has constantly clamps or is constantly clampless (i. e. in the non parthenogenetic form). This statement is, as we shall see later, somewhat too exclusive but it foreshadows the use of the clamp connections in systematics. As a taxonomic character, they were first used by Singer (1942) and Kühner (in a foot note on *Tricholoma* in 1937, and again in 1945).

The presence or absence of clamps is a very good and usually constant character that can be used for units as large as families (*Gomphidiaceae*, *Strobilomycetaceae*, *Russulaceae* — all three without clamp connections; *Paxillaceae*, *Hygrophoraceae* — both with clamp connections), and for genera (*Melanoleuca*, etc.), sections (*Omphalina*, *Lepiota*), species (*Pluteus atromarginatus* [Sing.] Kühner) and forms. In only very few species, the clamp connections are completely inconstant as well as scarce. This is the case in certain species of *Boletinus*, and in *Phylloporus rhodoxanthus*. Here, as in all characters, even the most useful ones, one can easily see that their value varies according to the group with which one is working. It often appears that the observer is not patient enough to search for clamp con-

nections, or not experienced enough to search for them at the right place If there are clamp connections, even in small number, anywhere in the carpophore but between hyphae cells exclusively (not at the base of the basidia), we may state that clamp connections are present. The best place for the search for clamps is a layer consisting of filamentous, thin, thin walled, not too densely interwoven hyphae; these are found, depending on the species, either in one of the covering layers — more commonly on the surface of the stipe than on the pileus, or in the basal tomentum, or in the hymenophoral trama, or in the tissue of the veil. A certain flexibility in the methods of the observer will be very advantageous. It should also be made a rule that a negative statement (clamp connections absent) should not be made unless at least several specimens from different locations have been patiently searched for clamps, and all septa observed have been found to be clampless. Doubtful (because of the early stage of the clamp formation or because of optical conditions) clamps should not be taken into consideration The clamps are either well developed at some septa, or not at all.

It is also important to keep in mind that occasionally, the clamps are formed in one tissue and not in another. This is especially true for densely interwoven layers consisting of thick walled hyphae, and in intricately agglutinated tissues of cortical layers. Here formation of clamps may be actually supressed rather than difficult to observe. In *Armillariella mellea*, a form is known that does not form any clamp connections in the carpophore up to the septum between the last subhymenial cell and the basidium, where a distinct clamp is formed. In *Cantharellula cyathiformis*, the mycelium has been observed to have numerous clamp connections, yet the carpophores are so constantly devoid of clamp connections, that this feature is used as one of the best characters for the distinction of this species. The opposite case (clamps present in carpophore - absent in mycelium) has also been observed in *Basidiomycetes*. It may well be assumed that those species with inconstant clamp formation as well as those where clamp formation has been abandoned except for a specific organ, can be considered as being in the evolutionary process of loosing the clamp connections as an unnecessary and uneconomical * way of cell division. It is therefore by no means surprising to find the transient species always in groups that, also according to the

* It is only fair to state that some cytophysiologists hold the opposite opinion

sum of their other characters, are intermediate between constantly clamped forms and completely clampless forms.

A further use of cytological characters derives from the fact that not all carpophores of the dicaryophyte have actually all single hyphae (i. e. the space delimited by wall and septa) binucleate. Hirmer, Brunswick and Kühner have shown that many hyphae and cystidia, especially the hyphae of the interior of the stipe, and the cystidia of such genera as *Pseudohiatula* often contain more than two nuclei, i. e. they are actually coenobial cells where the septum between the single dicaryons has failed to form. The number of the nuclei, in such cells, varies from 3 to 54. Kühner (1945) attributes considerable taxonomic importance to these multinucleate hyphae and cystidia, at least he uses it in phylogenetic arguments. Counting of the nuclei in these cells has not yet become a routine of the systematist but this may not always be so.

The so-called *Godfrinia* basidium, characterized by its development from a uninucleate basidiole, by the nuclear division taking place in the middle of the basidium (the basidium therefore attenuate above from a ventricose middle portion), and by the number of the sterigmata being two instead of four, with two uninucleate spores resulting, is not as marked a type as had initially (Maire, 1901) been suspected. It is merely the basidium of a parthenogenetic haploid of the genus *Hygrocybe*. The genus *Godfrinia* based on it by Maire, has been abandoned by all mycologists.

Another basidium-type, the *Lyophyllum*-basidium, has, in contrast with the *Godfrinia*-basidium, great taxonomic importance. It is characterized by the fact that — everything else being normal — the nuclei are not readily seen because of a dense granulation inside the basidia if aceto-carmine is used for staining. This kind of content is called carminophilous granulation (Pl. VIII). *Lyophyllum*-basidia, i. e. basidia with carminophilous granulation are found in all representatives of the tribus *Lyophylleae* in the *Tricholomataceae*, and according to Kühner, in some *Rhodophyllaceae*. A fragment of a not too young hymenophore is heated on a slide and kept moving in the medium which is the ordinary acetocarmine as used in cytological laboratories. When the first drop begins to evaporate and a film is beginning to form, the fragment is removed onto another slide; this is repeated twice, and the preparation is finally cooled off abruptly by putting the slide on a cold metal plate (microscope table); for stirring the fluid and for moving the fragment, a microscope needle is used

whereby enough iron is dissolved by the concentrated acetic acid of the acetocarmine to deepen the coloration of the contents of the basidia sufficiently, as far as the carminophilous granulation is concerned. This granulation is then blackish purple to violet-black and rather dense. The method results either in distinctly granular basidia or in non-granular basidia; intermediate cases are not known. Only *Lyophyllum connatum* does not show a very dense (yet satisfactorily distinct) granulation in adult basidia which is, however, absent in the basidioles. This method has the advantage of being applicable not only on fresh material but on well dried herbarium material.

The author found that the basidia with carminophilous granulation can easily be studied with morcein replacing acetocarmine, whereby the nuclei are colored in much the same way as with acetocarmine, yet the carminophilous granulation is invisible, the interior of the basidium is homogenized, and the nuclei and spindles are clearly distinguishable.

Still another aberration from the normal can be observed in some basidioles that remain sterile. The fusion and the divisions in those bodies do not take place in the ordinary manner; their contents are visibly non-protoplasmatic (hence their « empty » appearance), and at maturity, instead of forming spores, these bodies become slightly larger or otherwise insignificantly different in size or shape from the normal basidia. These bodies are called pseudoparaphyses (Pl. XII, 1; XIII, 1; XXVIII, XXIII). Their presence or absence, number, and distribution in the hymenium or on the edge of the hymenophore have a certain importance in systematics.

In very rare instances, concerning mainly tropical agarics, the last formed subhymenial cell, instead of becoming a basidium, transforms itself into a more or less isodiametric, often more or less sclerotized organ which cytologically corresponds to the basidium (see genus *Rhacophyllus* Berk.) yet, morphologically, differs in not forming sterigmata. Together with a more or less sclerotized cortical layer, it causes the carpophores to be more resistent to desiccation and postpones normal sporulation in favor of a higher degree of security for the organs in which reduction division takes place. This completely atypical behavior of some agarics is known as bulbillosis.

The indications given above show clearly that the cytological characters as such are either useless or of thus far unknown use for the purposes of the systematist. At the same time, some characters that are closely connected with the study of the life cycle, sexuality,

etc., yet not direct indications of any particular type of reproduction but rather « by-products » of the investigations on the latter, turn out to be of invaluable importance in taxonomy. The characters that are a direct expression of the sexuality of the *Agaricales* have not been studied in large enough number to allow any definite conclusions. It is not impossible (according to recent data by Quintanilha and others, 1941) that the future will give the two categories of spore polarity the standing of a character in specific or even generic taxonomy, but in the only genera where extensive studies have been made, viz. *Mycena* and *Coprinus* (the former genus was investigated by A. H. Smith, 1934, and Kuhner, 1938, the latter is since 1918 the favorite genus for sexuality research in *Basidiomycetes* because of easy culture methods and a wide variety of different behavior), the n polarity of the spores, homothallism, parthenogenesis, etc. did not show more than intraspecific constancy, and seem to be due to minor physiological mutations.

On the other hand, minor details of the main types of life cycles, prove to be of enormous taxonomic interest, e. gr. the location of the third division (sterigma or spore); the presence or absence of clamp connections in cases where they have no or little connection with the sexuality of the species; number of the nuclei in the voluminous coenobial hyphae and cystidia that cytologically function as merely another part of the dicaryotic system; presence of a granulation in the basidia that is colored by the same dye that colors the nuclei, incomplete or aberrant divisions in the basidiole leading to the formation of pseudoparaphyses.

Pigmentation of the cells

As an appendix rather than as an integral part of cytology, we shall now investigate another character that has to do with the anatomy of the interior of the cell and with cell physiology, i. e. the types and distribution of the pigments.

The rich and varied pigmentation of the *Agaricales* which surpasses by far that of the flowering plants implies the presence, in that group, of a large number of pigments, differing in regard to their chemical and physical particularities as well as their distribution on or in the hyphal (sporal, basidial, cystidial) wall or in the cell sap. Kuhner has made a special study (1934) of the topography of the colored substances (as he expresses himself in the title) of the agarics and boletes.

We shall here reproduce, in the outline, his classification of the pigments, and indicate examples for each type and subtype:

I. Intracellular pigments.
 a. Present in the living cell.
  1. Localized in the cytoplasma. *Cytoplasmatic Pigments.*
   (*Leucocoprinus luteus* yellow globules; *Inocybe geophylla* var. *lilacea* — uniform)
  2. Vacuolar. *Vacuolar Pigment* (Pl. XVIII, 4).
   (*Amanita muscaria*, *Bolbitius* [yellow species], *Leccinum aurantiacum*).
 b. Appearing after death of the cell.
   (*Callistosporium*, all species).
II. Membrana-pigment.
   (Elements of the cuticle of *Panaeolus sphinctrinus*)
III. Intercellular pigment.
   (*Naematoloma fasciculare*; *Lactarius griseus* and related species; *Paxillus involutus* [44]; *Suillus granulatus*; Pl. XXV, 9; XXVII, 5)

In a special chapter, Kühner shows that the topography of the pigments in the *Agaricales* has taxonomic value. It will become a more important factor in systematics, as soon as the number of single data, now accumulated (since Kühner's advice to taxonomists to describe the pigments observed) has grown sufficiently. Even now, in many genera, species can be most clearly distinguished by the type and location of the pigment. Naturally, in many cases, two or more different types of pigments are combined either in the interior of the cells, or in the wall, or intercellularly. For instance, the reaction with H_2SO_4 observed on the spores of certain *Coprinaceae*, and indicated above under « microchemical reactions », shows that there are two different kinds of pigment in these spores, one soluble and one insoluble in sulphuric acid. The same is true with pigment combinations in the cuticle of certain *Russulae* (*Russula* red and *Russula*-yellow often combined). There may also be combinations of vacuolar and membrana pigment, and vacuolar and intercellular pigment, and membrana- and intercellular pigment (e. gr. in the boletes). It is often difficult to decide whether a pigment is membranal or intercellular-incrusting (« epicellular »). It is a feature of the intercellular pigment to be easily dissolved (either after decoloration, or with a change of color when dissolving, or without any color change) in alcohol, ammonium hydroxide, even in water. Only few epicellular pigments are

[44] Atrotomentine, a 2 5 di para-oxy-phenyl-3-6-di-oxybenzochinone has been analyzed and later synthesized by Kögl. It is the intercellular pigment of *Paxillus atrotomentosus*

insoluble in these solvants, and these are readily recognizable as superficial (e. gr. the resinous crust responsible for the colored crust on top of the colorless wall of the cystidia in some boletes). On the other hand, the true membrana pigments even though they have the appearance of epicellular pigments because of the lack of elasticity of the outermost, strongly pigmented layer of the wall which then breaks off into fragments (spiral or areolate ornamentations), are always insoluble except in such rude solvants as concentrated sulphuric acid.

XVI. PLANT GEOGRAPHY AND ECOLOGY

Plant geography and ecology of the fungi, and especially the *Agaricales* are so enormous in their theoretical and practical significance, so wide and ramified in spite of the superficiality of most of the data available, they can not really be treated here. However, the influence of data of this order on problems of taxonomy is too obvious to be ignored. There are all shades of opinions on the question whether or not the *Agaricales* have definite areas determined by the climate and its changes in history of plant life as admitted for *Cormophyta*. It shall not be denied here that the average geographic area of a representative of the *Agaricales* may be larger than the average area of an angiospermous plant. (It should likewise not be denied that the average area of an angiosperm is larger than that of an insect). But we have, in the *Agaricales*, everything from pantropical species and pantropical genera to endemics on tiny islands; we have typical vicariants, geographic races (which we call subspecies) that are fully the same as the geographic races of the phanerogams. The larger spores of the European *Suillus granulatus* showed it to be the type subspecies of a « circle of races » that was determined not merely by geography but also by mycorrhizal relationship: The American form was connected with 5-needle pines, and the European one with 2-needle pines.

Here, we have a characteristic correlation between the fungus-host-relationship and the climatic factor. A form that differs from the other only in the host, not in geography, is called a mycoecotype (Singer, 1940), if, of course morphological differences are also present. Otherwise, the distinction is based on experimental transplantation exclusively which would not be conclusive for *Agaricales* as much as

it is for *Uredinales* (where the mycoecotype without morphological differentiation is known as ecological form).

It is quite obvious that the host-relationship, often taking the form of mycorrhiza partnership, is an important taxonomic factor since it often caused a regional if not geographic separation of the races involved and an independent evolution of both ramifications of the system in many cases. There is evidently a basic difference between the *Gymnopili* on frondose trees, on *Monocotyledones*, and on conifers. There is also a significant difference between the primitive *Russulae* and *Lactarii* that are non-mycorrhizal and the higher forms that are mycorrhizal and even specialized. The *Sphagnum*-Galerinas appear to form a definite group, and the constancy with which the *Suilloideae* confine themselves to mycorrhiza with conifers is undoubtedly no less impressive than the near unanimity with which the *Leccina* favor the *Fagales* and *Salicales*. No less striking as a constant conifer-mycorrhiza, is the entire family *Gomphidiaceae*. Other ecological groups distinguish themselves by a prominence of forms preferring open places (outside the woods), gardens, greenhouses, lawns (e. gr. most of the *Bolbitiaceae*, which, even where entering the woods, never were found to form mycorrhiza). It is undeniable that all these ecological groups are at the same time taxonomic groups. Consequently, we feel safe to cite geographic and ecologic differences and similarities as auxiliary characters, supplementing and sometimes explaining the morphological and chemical characters.

It is too early to be very precise about the geographic areas and the ecologic characteristics of all the groups. The data available are though by no means too scattered, yet, unfortunately, too unreliable. A citation of an agaric or bolete, without study of the specimen, by anybody less than a first rate specialist, is not a scientific document of any weight. Reducing our material by elimination of the doubtful, we finally arrive at a point where the material begins to become so scarce that, in some cases, conclusions can no more be drawn, and even in the remaining cases this can be done only in the three or four best herbaria of the world.

Under these circumstances, speculative theories, area maps, and conclusions reaching far beyond the available evidence have often been published, recently even on boletes. An improvement on the taxonomic methods, more collections, and less reliance on literature sources will eventually show that the boletes are an excellent field

for those who are interested in the mycological aspect of historical plant geography, and the evolution of the species in fungi. Only the richness of a large herbarium, with a few genera worked out according to the standards of modern taxonomy, will circumscribe clear areas, and even these will be corrected by further planned collecting in the border regions.

PHYLOGENETIC THEORIES CONCERNING THE ORIGIN OF THE AGARICALES

The phylogeny of the *Agaricales* is a strongly controversial field. The history of phylogenetic systematics of the *Agaricales* has been analyzed at length in a previous paper by the author [47]. It is intended to give, in the present chapter, an account of the arguments used and the views expressed in accordance with the facts now available. The accumulation of facts, found in a search for supporting data for one's own hypothesis, or for the purpose of invalidating an opposing argumentation, would in itself be justification enough for the serious discussion of this subject — a subject that seems to be so utterly « theoretical » for some scientists. It is generally acknowledged that only paleobotany can ultimately prove the direction of progress and regression, yet all the other available data taken together often give a rather convincing picture of the evolutionary trends in certain groups, and only those who refuse to recognize it because of prejudice against evolutionary theories in general, will deny the high degree of probability in certain parts of the phylogenetic schemes proposed.

Among the facts brought to light in comparatively recent times, we have to mention the connection existing between certain *Gastromycetes* on one hand and certain *Agaricales* on the other hand, and between certain *Agaricales* on one hand and certain *Aphyllophorales* on the other hand. It will be enough to study the whole series of forms between the extreme *Astrogastraceae* and the extreme *Russulaceae* as has been done by Buchholtz (1902), Lohwag (1924), Malençon (1931), Heim (1938) and Singer (1936-1939), or the series from *Cyttarophyllum* to *Galeropsis* (Singer, 1936), or from *Truncocolumella* to *Gastroboletus* and *Boletinus decipiens* (Malençon. 1938, Zeller, 1939,

[47] R. SINGER, *Das System der* Agaricales. *Ann. Myc.* 34 . 286-378, 1936.

Singer, 1942-1945), or from *Montagnites* to the *Coprinaceae*, in order to lose all illusion about the sharpness of the key characters allegedly distinguishing the *Gastromycetes* from the *Agaricales*.

On the other hand, real or apparent transitions from the *Aphyllophorales* to the *Agaricales* were suggested in large number in order to satisfy the hypotheses — dominant at times — of derivation of the *Agaricales* from the *Aphyllophorales*. The collapse of all the speculation about a relationship between the *Boletaceae* and the *Polyporaceae*, based by Neuhoff & Ziegenspeck on a *Gyrodon* with allegedly white spores, and by others on Höhnel's white-spored *Filoboletus*, is now complete. The *Gyrodon* turns out to be *Boletus edulis*, and its spores are not white but — absent, and the *Filoboletus* turns out to be a poroid form of the marasmioid *Tricholomataceae*. A careful revision of the tramal structure of all *Strobilomycetaceae* and *Boletaceae* (Singer, 1945) has established the fact that all boletes have more or less bilateral hymenophoral trama, a structure unknown in the *Polyporaceae*. White spore print also does not exist in the *Boletaceae* and *Strobilomycetaceae*, and the genus *Leucogyroporus* was based on an erroneous observation by Murrill, while *Polyporoletus* Snell turned out to be a *Scutiger*.

However, other connections between the *Aphyllophorales* and the *Agaricales* have been uncovered recently. The author does not enter the argument about an alleged affinity between *Cantharellus* and *Hygrophorus*. It may be enough to say that a collective group, an assemblance of notoriously unrelated species, such as Fries's genus *Cantharellus*, can be used to prove the affinity with numerous other groups, exactly as many as there are represented in the collective genus in the first place. While there are elements of *Clitocybe, Hygrophoropsis, Leptotus, Geopetalum, Cantharellus, Gomphus*, to name only a few — there is, as far as is known to the author, no representative of the *Hygrophoraceae* hidden in *Cantharellus*. Should it have been the bright yellow-orange or red color of some *Cantharelli* and some *Hygrophori* that first suggested the affinity ?

But there is an affinity between *Lentinus cyathiformis* and the genus *Polyporus* (sensu stricto). Kühner (1929) gave several valid reasons, and Bondarzew & Singer (1941) added more. Donk stated (1933) that the whole genus *Lentinus* should be treated taxonomically in continuation of *Polyporus*; but since he did not at the time offer any additional proof, it seemed possible to think that only *Lentinus cyathiformis* was affected by Kühner's comparison. Donk's statement, how-

ever, proved correct in another sense. A detailed anatomical study of the trama and subhymenium of *Pleurotus, Panus,* and *Lentinus* reveals that each of these genera has its counterpart, anatomically, in the genus *Polyporus* (sensu stricto) (*Favolus, Pseudofavolus*). Some of the species of the genus *Polyporus* are distinguishable from the corresponding *Pleurotus, Panus,* or *Lentinus,* mainly by the configuration of the hymenophore. The latter, however, has ceased to be considered as of great weight since the close relationship between *Xerocomus* sect. *Pseudophyllopori* and *Phylloporus* has been established on the basis of anatomical and chemical data (Singer, 1945), since a more detailed study of the false, agaricoid *Laschiae* by Singer (1945) and Heim (1946) revealed that Van Overeem (1926) was right in attributing to some tropical agarics a tendency to transform the configuration of their hymenophore, step by step, from lamellate to tubulose. In the light of these data, it appears that there is actually no appreciable gap between *Lentinus, Panus, Pleurotus* on one hand, and *Polyporus, Favolus, Pseudofavolus* on the other hand.

In the same investigation of the types once referred to the so called *Laschiae*, Singer (1945) attempted to draw a line between the true *Agaricales* (*Dictyopanus, Filoboletus,* and especially *Poromycena*) and the other laschioid *Basidiomycetes* (excluding the original *Laschia* which belongs to the *Auriculariaceae*) which were considered as belonging in the suborder *Cyphellineae* in a wide sense. It was also said, in the same paper, that certain *Tricholomataceae* with always lamellate hymenophore, such as *Panellus, Hohenbuehelia, Asterotus,* and perhaps *Schizophyllum* might perhaps be close to a group deriving from these cyphellaceous genera rather than from any *Gastromycetes*. Since it now appears that the *Cyphellineae* themselves are a rather artificially mixed group (Donk, *ined.*), they have lost their phylogenetic importance as a starting point, and *Favolaschia* becomes solely allied (though not closely) to *Aleurodiscus* unless more facts supporting the connection between *Favolaschia* and *Dictyopanus* become available in order to make the bridge between *Favolaschia* and the *Agaricales* something more than speculative. By the same token, *Campanella* and *Leptotus* are rather isolated agaricoid branches of aphyllophoraceous groups, and unless more evidence is brought to light, to substantiate the speculative bridge one may be tempted to construct between *Leptotus* and *Omphalina* on one hand, and between *Campanella* and the *Resupinateae* (*Tricholomataceae,* genera *Resupinatus* and *Hohenbuehelia*) on the other hand — such

connections between the *Aphyllophorales* and *Agaricales* must be considered as possible but not as probable in the same degree as the bridge *Polyporus-Lentineae*, or the bridges indicated between *Agaricales* and *Gastromycetes*.

All these affinities, assumed or otherwise, make the question timely again that has been asked before: What exactly are the limits between the *Agaricales* and the neighboring orders of *Basidiomycetes*? It has come to the point where the answer to this question cannot be given by an agaricologist alone but it is a problem that must and will seriously concern those working on *Aphyllophorales* and *Gastromycetes*. We agaricologists want to have help in the important decision that lies in the answer to the questions: Is there (and where) a sufficient gap between the genus *Polyporus* and the remaining polypores? Is there (and where) a line between the *Secotiaceae* of the *Galeropsis* group and the «true» *Gastromycetes*; is there (and where) a line that can be laid between *Rhizopogon* and the other boletoid *Hymenogastrineae* on one side, and the «true» *Gastromycetes* on the other; is there (and where) a sufficient gap between the *Astrogastraceae* on one hand and the remaining *Gastromycetes* on the other hand?

There are those who doubt that there is such a gap inside of what was formerly considered a solid group — the *Aphyllophorales*.

There are those who doubt that there is such a gap in what was formerly considered — if not a natural group — a strongly convergent group of strictly parallel lines, the *Gastromycetes*.

If both are right, i. e. if there are no gaps in either case, and the three groups intergrade with each other without so much as an appreciable hiatus, there are only three alternatives for the phylogeny of the *Agaricales*:

1. The *Agaricales* are interpreted as an intermediate group between the *Aphyllophorales* and the *Gastromycetes*, with the *Aphyllophorales* the starting point, and the *Gastromycetes* the summit.

2. The *Agaricales* are an intermediate group between the *Gastromycetes* and the *Aphyllophorales*, whereby the former are considered as the starting point (or points), and the latter as the «summit».

3. The *Agaricales* are a genuinely polyphyletic group with one part derived from the *Aphyllophorales*, the other from the *Gastromycetes*.

The hypotheses (1) and (2) have the disadvantage of suggesting that the evolution supposed to have taken place, runs in an immense

circle. In fact, starting as we do, from the assumption that no convincing dividing lines between *Agaricales*, *Aphyllophorales*, and *Gastromycetes* exist, we have to admit that the only reasonable derivation of the *Gastromycetes* as a whole is that outlined in rare concordance by nearly all specialists of the *Gastromycetes*, i. e. an evolution starting at a low point of the *Aphyllophorales* system, and running parallel with the *Tuberales* of the *Ascomycetes*, finally reaching the most highly developed, unipilous forms of the *Phallineae* and the agaric like *Secotiaceae*, *Hymenogastrineae*, etc. If, then, no gap is allowed between the *Agaricales* which would be derived from the *Gastromycetes*, and the *Aphyllophorales*, the latter would become merely strongly reduced agarics, step by step sinking backwards and downwards to the level where the *Gastromycetes* were supposed to have started. The same (vicious) cycle results if the direction is reversed.

Hypotheses (1) and (2) are therefore not popular at present, and it would take the discovery of a whole series of entirely new and unexpected facts to ever revitalize them.

This leaves more or less intact only the theory of polyphyletic derivation of the *Agaricales* — always assuming that there are no gaps either in the *Aphyllophorales* versus *Polyporus*, nor in the *Gastromycetes* versus *Galeropsis*, *Hydnangium*, *Truncocolumella*, etc. To this theory, we may add the two other possible theories, one based on the conviction that a gap between the *Agaricales* and the true *Aphyllophorales* does exist, and the other based on the conviction that a gap between the agaricoid *Gastromycetes* and the true *Gastromycetes* does exist.

Consequently, the three logically possible, and actually important theories, of today, each of them defended or favored by a group of systematists, are the following:

I. [(3) of our previous scheme] Derivation of the *Agaricales* from the *Gastromycetes* and from the *Aphyllophorales*.

II. Derivation of the *Agaricales* from the *Gastromycetes* alone.

III. Derivation of the *Agaricales* from the *Aphyllophorales* alone.

It cannot be stated at present that the probability of one of these theories is overwhelming as compared with the others. A taxonomist, after enough practical experience, can only give one a slight edge over the others, expressing a preference. In spite of the author's preference for theory II, the attempt will be made to state the case for each of them.

We shall start with the theory that has a slight majority of mycologists on its side because it is the oldest and most deeply rooted in the mind of mycologists, i. e. theory III which, it seems, can be linked with the name of Fayod (among many others in his generation), Neuhoff and Gäumann.

DERIVATION OF THE AGARICALES FROM THE APHYLLOPHORALES

The author has the strange task to revitalize a theory that was originally based on the faulty assumption of a bridge between *Polyporus* and *Boletus*, and another between *Cantharellus* and *Hygrophorus*. However, it seems that the same result will be obtained if more reasonable suggestions are followed up. For example, one may assume that the line leading to the higher tropical polypores of the genus *Microporus* continues by the way of *Microporellus* Murr. and finally reaches into the genus *Polyporus* sensu stricto, whereby the turning of a poroid hymenophore into a lamellate hymenophore would be merely a repetition of an analogous development in the *Daedalea-Daedaleopsis-Xerotus (Gloeophyllum)* group and in the *Coriolus-Lenzites* group. It may also be assumed that *Leptotus* (that may be derived from a corticiaceous or meruliaceous source), by a growing differentiation of its trama finally achieves an elevation to a level that makes it comparable with *Omphalina* (especially its pleurotoid representatives with which it has some external similarity). Finally, it may be assumed that *Favolaschia* is something like a halfway mark between *Aleurodiscus* and the *Tricholomataceae*, and it may then be considered as possible that the direction of the evolution is from *Aleurodiscus* to the *Tricholomataceae*. These three potential bridges do not necessarily exclude each other; they may be parallel.

This manner of seeing the interrelationship between certain borderline *Aphyllophorales* and the *Tricholomataceae* — only these are concerned — recognizes and explains the similarity between the structure of the cortical layers in *Favolaschia* and *Mycena, Campanella* and *Asterotus*; it also explains the presence of gloeocystidia in *Agaricales* such as *Lactocollybia*, and the gelatinous strata in the *Resupinateae*. It explains furthermore the presence of forms with tubulose hymenophore in the *Tricholomataceae*. The round dendrophyses of *Favolaschia*, especially those with vacuolar pigmentation, and the diverticulate hyphae of some of its species are found

again in *Mycena* which also has the amyloid spores of that genus.

The other families of the *Agaricales* must all branch out from the *Tricholomataceae*. There is no other choice in this scheme. The thicker walls in spores like those of *Phaeomycena* would perhaps lead to the *Crepidotaceae*, and the genus *Ripartites* may also be considered as transitional between *Tricholomataceae* and *Crepidotaceae*. From the *Crepidotaceae* one line would lead to the *Cortinariaceae*, and one to the *Paxillaceae*. This necessitates the assumption that the *Boletaceae* derive from lamellate families. The line from the *Tricholomataceae* to the *Cortinariaceae* may also lead by the way of *Ripartitella* and *Cystoderma* to the *Agaricaceae* and from *Cystoderma* to the *Cortinariaceae* (via *Phaeolepiota*), or by the way of *Leucocortinarius*. The *Amanitaceae* would be the terminal of a branch leading from *Armillaria* to *Catathelasma*, and from there to *Amanita* and or from certain pleurotoid groups to *Rhodocybe* and further to the non volvate *Amanitaceae*. The insertion of the *Hygrophoraceae*, *Rhodophyllaceae*, *Bolbitiaceae*, *Coprinaceae*, and *Strophariaceae* would perhaps cause certain difficulties but this can be considered as a minor problem.

All the possible ramifications of the descendants of the *Aphyllophorales* are possible on the presumption that a progressive development with a tendency to complication of the gross structure and the anatomy of the *Agaricales* takes the lead. The spores become gradually pigmented (mostly with a membrana pigment which is still absent in the early stages of spore development and arrives at its peak at maturity), the layers of the wall become more and more complex, and the originally smooth spores become ornamented. The originally inconspicuous carpophore becomes larger in size (at least where the *Campanellae* and *Favolaschiae* are envisaged as ascendants of *Agaricales*), or at least more regularly stipitate, or the pseudostipe of *Microporus* becomes a true stipe in *Polyporus*, or is replaced by a stipe. The stipe in the soil inhabiting forms becomes central, the veil develops gradually from simple and rudimentary to double and well developed.

At a certain stage of development, a tendency of the agaricoid carpophores toward angiocarpy begins that ends up in making them gastromycetoid. Under the influence of arid climates, the pileus remains closed until after the maturity of the spores, and this, automatically relieves the hilar attachment from its functions of forceful spore discharge and the spores become orthotropic. This leads to

strong convergence with another series of true *Gastromycetes* which have become angiocarpous at a much lower level of development. A similar convergence must explain the russuloid and the boletoid *Hymenogastrineae*.

The advantages of this scheme are: Easy placement of the *Leptotaceae*, elegant disposal of progressive lines leading towards groups with more complex structure; ecological explanation of the genera *Montagnea, Galeropsis*, etc.

The disadvantages are: Difficulties to explain the derivation of the *Russulaceae*. If hard pressed, one may indicate *Melanoleuca* as starting point of that family but the characteristic heteromerous structure of the trama, the macrocystidia, and the bright pigmentation would remain unexplained (as well as the absence of lamellulae in the higher *Russulae*, an otherwise unheard-of development). This situation would become worse if any hymenogastraceous forms are admitted as further ramifications of the *Agaricales*-system. This would lead to the assumption that forms with clamp connections are derived from forms without clamp connections, and the beautiful structure of progressive development within the *Agaricales* proper would appear to be gained at the expense of an unlikely line of «degradation» (loss of the amyloidity of the spores, loss of the stipe, loss of the regularity of the hymenophore, etc.) as soon as the gastroid field is entered. Another disadvantage of this scheme must be seen in the fact that the progressive development toward more complex structures as expressed in the formation of one or more layers of veil formations is left without a biological background. If the biological explanation of the veil is — a preliminary stage to angiocarpous development, then, nobody will understand why this should be started in a slow way — long before the level is reached at which the actual transition into gastroid forms can take place. This reasoning is not only un-Darwinistic but contrary to any kind of logic. The alternative is to assume that veil formations, volva, cortina, pellicular veil, and marginal veil are all of advantage to the conservation of the species in one way or another. How that could be the case — we do not know.

DERIVATION OF THE AGARICALES FROM THE GASTROMYCETES

In the *Russulaceae*, the nests of sphaerocysts can be interpreted by the fact that in the process of transferring the fertile zone of the hymenophore downwards and carving out lamellate instead of loculate hymenophores, the hollow spaces would be filled in by «overgrowings» of the hymenial covering, the elements pushing against each other and thus forming a pseudoparenchymatic tissue enclosure according to the rule explaining the formation of the sphaerocysts in the annulus superus of *Amanita* and certain organs of the Phalloids. The pseudoangiocarpous development of some *Russulae* and *Lactarii* is explained as the reproduction in the primordial stage of the development of some hymenogastraceous fungi which have a gymnocarpous earliest stage which is followed by a prolonged angiocarpous stage and a post maturity stage with naked gleba or partly exposed gleba. The spores, originally orthotropic and mostly globose with prominent fundamental ornamentation, become at first slightly heterotropic but still remain so strictly globose that it is difficult to see their axial asymmetry; their exosporial ornamentation becomes comparatively more and more important; eventually, the spores become somewhat elongate, and truly heterotropic with the ornamentation so covered up with the exosporial ornamentation that the latter is no more recognizable without dissolution of the amyloid portion. At the same time, the spores become more yellow, the mycorrhiza relationship more constant and more selective. Veils that in the first stage have appeared in consequence of the pseudoangiocarpous development are lost in the higher forms because of abandonment of the angiocarpous phase as a reminiscence of the angiocarpous development of the *Astrogastraceae*. The clamp connections, still occurring in some of the gastroid forms, are entirely lost in the genus *Russula* as well as in *Lactarius*.

Some of the characteristic features of the gastroid group are retained in the *Russulaceae*. These are, among others, the fleshy granulose consistency, the presence of pseudocystidia, the white to yellow color of the short, ornamented spores, the bright pigments of the peridium and the presence of a latex in many forms. In lower groups (*Russula delica*) «poroid» — actually gastroid — aberrations of the hymenophore are still common, in higher groups they are rare.

Another line running in the same general direction (gastroid agari-

coid), has been found in the *Rhizopogon-Chamonixia Truncocolumella-Gastroboletus-Boletinus decipiens* (gastroid condition) line. Here, too, the spores are basically similar in both groups, the banded spores of *Chamonixia* (finding their counterpart in some *Strobilomycetaceae*) and *Truncocolumella* coming so close to gastroid conditions of *Boletinus decipiens* that their only principal difference consists in orthotropic spores in *Truncocolumella*, and heterotropic spore formation in the *Boletinus*. In this case, the arrangement of the cavities has been changed into a regular hymenophore rather than abandoned and filled out as in the *Russulaceae*. Consequently, there is no heteromerous tissue here, but the tendency to bluing by autoxidation *(Chamonixia, Porphyrellus)* or reddening by wounding *(Rhizopogon, Strobilomyces)* is common in both groups. Clamp connections are still found in the agaricoid group but they evidently soon disappear in the higher forms. On the other hand, the formation of obligatory and specific mycorrhiza goes further back in the gastroid line, and is probably typical for all *Strobilomycetaceae* and *Boletaceae*. The trama of the walls between the loculi in *Rhizopogon* is distinctly bilateral (as in many *Gastromycetes*), yet with the medio-and lateral stratum not as well differentiated as in the higher *Boletaceae* and *Strobilomycetaceae*, the outer layer not being gelatinized. The subhymenium is very similar to that of the *Boletaceae* with catenulate short rectangular to almost cubic cells predominating. The pigments are membrana pigments and epimembranal pigments in the peridium and in the cuticle of the pileus in most Rhizopogons and boletes, and these pigments are not easily dissolved in either case. We find that the host range of certain parasites is limited to *Rhizopogon*, boletes, and *Paxillus* (Heim, 1934).

In both cases, i. e. in the *Astrogastraceae Russulaceae* line and in the *Rhizopogonaceae-Boletaceae* line, by far the more numerous, more varied, and as a whole more widely distributed group is the agaricoid group. This is considered as an indication that the direction from gastroid to agaricoid forms is more likely to be true than the reverse, if such an additional indication is still necessary. This direction is very important because — if it is accepted as probable in one case, it becomes very suggestive as a general principle, even in groups where the derivation from the *Gastromycetes* is still entirely speculative, e. gr. in the connection suggested by Romagnesi between *Richoniella* and *Rhodophyllaceae*, in the connection suggested by Maublanc between *Battaraea* and *Agaricaceae*, in the connection suggested as a

possibility by Singer between *Torrendia* and *Amanita,* and in the undoubtedly existing connections (but without a clear indication of the direction of the phylogenetic trend) between *Galeropsis* and *Bolbitius,* and between *Montagnea* and *Coprinus.*

The remaining *Agaricales* may be derived from any of these *Gastromycetes*, or from the bolete branch which shows some tendency at certain levels to form lamellate hymenophores (or perhaps, the original hymenophore, as in *Russula,* was lamellate, and the evolution of the tubes was secondary) and these lamellate groups though still distinctly showing their affinity with boletoid forms (*Paxillus-Gyrodon ; Phylloporus-Xerocomus ; Gomphidius-Suillus)* begin to abandon the mycorrhizal specificity in favor of lignicolous habitats and saprophytic nutrition, or to complicate their dependence on mycorrhiza by acquiring a double dependence *(Gomphidius).* Another step would lead to the *Crepidotaceae*, and from here to the *Cortinariaceae*, *Tricholomataceae* and *Rhodophyllaceae.*

A separate derivation of certain other groups, such as the *Agaricaceae*, *Amanitaceae*, and *Coprinaceae*, is also warranted because of the volva which is in this scheme not considered as a useful acquisition by highly developed agarics but rather as a reminiscence from gastromycetous ancestors for which the volva evidently was an additional adaptation. This becomes clear when (1) the fact of the existence of many transitions between a compact volva and volva rudiments is considered which can much easier be explained by reduction of the volva than by progressive acquisition ; (2) when it is understood that the truly volvate species, even in *Amanita* are a small minority, and that *Amanita muscaria*, occurring far to the north under tundra conditions, as well as *Amanita nana,* occurring in the steppes and semideserts of Asia, both have reduced volvae whereas the truly volvate *Amanita caesarea* occurs in warmer temperate regions not only in the comparatively dry mediterranean zone but in the humid zones of the Colchic district and in Eastern North America. The number of truly volvate *Amanitae* is higher in ancient floras that have remained undisturbed during a long period such as many tropical regions in southeastern Asia. The fact that *Amanita* shows a rather high development in other regards than the volva can only be explained by the fact that the *Amanitae* originate in a series of genera other than the nonvolvate agarics with a lower organization in other regards. These indications of a higher level are (1) absence of clamp connections in many species (2), binucleate spores in all

species studied, (3) amyloid spores in more than half of the species — though rarely in species with a complete unreduced volva of the *caesarea* type. It is, however, impossible to link all these characters with the presence of a volva. Another genus with double veil, *Catathelasma*, has numerous clamp connections and uninucleate spores in all species known.

If the search for gastromycetous ancestors of the families of *Agaricales* leads to desert species, it is not assumed that they themselves, highly organized and rather specialized as they are, represent the very ancestral forms from which our recent *Agaricales* have immediately derived. But we assume that it was from forms of the same general type as those deserticolous *Gastromycetes* that they may have derived, viz. from non-mycorrhizal forms becoming mycorrhizal, or from non-coprophilous forms becoming coprophilous. It is not pretended that parts of a desert flora have given rise to a typical forest flora.

Advantages: This theory is able to explain all the facts known in the *Russulaceae* and the boletes. In this regard it is perfect — as far as any theory based on non-paleobotanical material exclusively can be perfect. The scheme for the remaining families, though essentially hypothetical, has the advantage of pointing at a possible solution that is, in its general tendency from angiocarpous to gymnocarpous forms as admitted in the *Russulaceae* and boletes, completely conform with that in the latter two families. It also explains the veils more satisfactorily than the other theories.

Disadvantages: It cannot in detail explain the derivation of the *Amanitaceae* and a few other families, and is handicapped by the complicated manner by which it attempts to explain the xerophilous character of some of the supposedly ancestral forms of the *Coprinaceae* and *Bolbitiaceae*. It leaves unexplained the similarities between the genera *Campanella* and *Favolaschia* on one hand and certain *Tricholomataceae* on the other hand unless the latter two genera are considered as reduced and atypical members of the *Tricholomataceae* (as has virtually been suggested by Patouillard).

The derivation of the *Agaricales* from the *Gastromycetes* has been first indicated by Brefeld, on the basis of general considerations of the structure of both these groups; later it was adopted by Buchholtz on the basis of his data on *Elasmomyces* and *Archangeliella*. Höhnel accepted Brefeld's view, and Lohwag accepted and elaborated on Buchholtz's theory. Singer (1936) brought his new classification in

agreement with this theory and accepted it in detail for the whole order. It woud, however, be incorrect to say that a classification is entirely based on a phylogenetic theory. Neither the classification of 1936 nor the modifications admitted in this book, are the result of phylogenetic deliberations but, vice versa, the phylogenetic theory is the result of taxonomic data.

While the theories of a derivation of the *Agaricales* from the *Aphyllophorales*, and the derivation of the *Agaricales* from the *Gastromycetes* have often been linked with a specific complete classification of the *Agaricales*, this has never been the case in regard to the last, remaining theory, that of a derivation of the *Agaricales* from both the *Aphyllophorales* and the *Gastromycetes*. In fact it is rather difficult to cite authors who have expressed their views in exactly this way. While a certain degree of polyphyletism is admitted by many mycologists, it has never been said, except by implication, that part of the *Agaricales* were derived from the *Aphyllophorales*, and part from the *Gastromycetes*. Yet, if it is allowed to piece together various statements by C. Dodge, perhaps also R. Maire at certain periods, and R. Heim p. p., it will be corret to consider these authors as in favor of a polyphyletic derivation of the *Agaricales* as specified above.

DERIVATION OF THE AGARICALES FROM BOTH GASTROMYCETES AND APHYLLOPHORALES

Assuming that the derivation of the *Russulaceae* and boletes from hypogeous *Gastromycetes* is sufficiently substantiated, it would here be considered as possible to separate completely these two families and any such groups that may have derived from them immediately (e. gr. *Strobilomycetaceae*, *Paxillaceae*, *Gomphidiaceae*), from the rest of the *Agaricales*, especially the white spored group (*Tricholomataceae*) which would then be derived from the *Polyporaceae* and or the *Leptotaceae* or parts of these families as has been pointed out above.

Advantages : At the present stage of our knowledge, this scheme presents all the advantages of both preceding theories, and avoids some of their disadvantages. It reflects the wise and conservative attitude under the given circumstances.

Disadvantages : As all « eclectic » theories, it is somewhat inco-

herent and inconsistent. It appears to be objectionable to allow an evolution from angiocarpous to gymnocarpous in one case, and from gymnocarpous to angiocarpous in another case. Though it may be argued that it is undoubtedly true that both these developments have taken place in the evolution of the fungi at one place or other, and nothing forbids a priori to believe that this has also happened within the *Agaricales*, it is nevertheless bewildering to find the veil assuming one rôle and designating one direction of evolution while — almost simultaneously — the same organ plays the opposite rôle and the general trend seems to run in the opposite direction. Besides, a more practical disadvantage would arise, one that has probably prevented those in favor of this theory to ever link it with an elaborate classification of the *Agaricales* : this practical disadvantage is the necessity, in any classification, to draw a dividing line between the two main groups of *Agaricales*, those derived from the *Aphyllophorales*, and those derived from *Gastromycetes*. Since the taxonomic data at hand do not warrant such a sharp dividing line, it would be necessary, probably for a long time to come, to maintain the division into fifteen families rather than to attempt a new bipartition of the *Agaricales*. If this bipartition should have removed only the *Russulaceae* from the bulk of the *Agaricales*, it would have been easy to do so on the basis of a large number of excellent facts. But there is, in systematics of the present day, absolutely no way to find a common denominator for a group that is left over after both *Russulaceae* and the boletes with « appendages » have been removed.

Future research will perhaps give more weight to one of the three schemes outlined in this chapter — or possibly advance a fourth.

PROBLEMS OF NOMENCLATURE

The problem of nomenclature is not a subject in itself as far as the present work is concerned but it becomes an important factor in the choice of the correct names to be adopted. The author is fully aware of the fact that here, more than in any special paper intended primarily for specialists, the correct choice of the fungus names is a great responsibility. The bibliographical work involved will only be appreciated by those who are familiar with the difficulties of the strict application of the International Rules of Nomenclature in mycology. The difficulties lie not so much in the following of the

rules as in the handling of cases that are not foreseen in the Rules of Nomenclature. It is necessary in all cases to follow the rules and even the recommendations have been followed to the letter. Certain provisions of the Rules, however, are in need of further clarification by an International Congress and some articles, especially those referring to the starting points of mycological nomenclature are subject to a difference in interpretation that causes more divergence of nomenclature in specific cases than is generally realized.

Two very important problems, those concerning the typification of the genera (« nomina lectotypica ») and the conservation of generic names are practical problems that require a thorough examination of the cases from all angles and, afterwards, the proposition of a list of lectotypes and « nomina conservanda » for acception by an International Botanical Congress. Such lists have been proposed for adoption by Singer, R. & A. H. Smith (1946), and since these are the only approximately complete lists that can be used in the *Agaricales*, the nomenclature of this book is based on these lists. The genera that are not mentioned in these lists are either typified by their authors, or they are monotypic, or else do not constitute a taxonomic problem at present. The « genera conservanda proposita » by Singer & Smith are here treated as if they had been accepted already since this seemed to be the only possible consistent policy.

A third problem is very difficult. It concerns the habit of all modern taxonomists who follow the rules at all, to consider a pre-Friesian name, validated according to Art. 20, *e f* by a post-Friesian author as based on the specimen or description of the latter. It is, as has been pointed out to me by M. A. Donk in a very interesting discussion on the subject, rather questionable whether or not this customary procedure conforms with the intention of those who voted the original rules in 1910. Nevertheless, it would be grossly unfair and detrimental to the general acceptance of nomenclatorial rules, if those who have adhered to them as they best understood them, were now penalized by a revision of the interpretation or, if one wants to express it so, by a reconstitution of the original intentions. From a practical point of view, the admission of the original pre-Friesian author's concept as the type of a (re-) validated name would contribute toward a better documentation only in the case of Persoon (and even here not in all cases); in the case of other authors, especially Scopoli, Schaeffer, Bulliard, Withering, Linnaeus, Batsch, Bolton, etc., it would open the door for futile discussions and a variance of inter-

pretation which would be especially dangerous and detrimental in cases where the Friesian name is already fixed by a more methodical description, or by unanimous tradition. This should be avoided, and can be avoided; for, the decisive factor is Art. 5 which says that « in the absence of a relevant rule, or where the consequences of rules are doubtful, established custom must be followed » [18]. Since it is obviously established custom, at least among those who follow the rules at all, and the consequences of Art. 20, *e* and *f*, are doubtful in the light of Art. 18 (Type Method) which has been added later, it must be assumed that Art. 5 applies here. Consequently, the author does not admit pre Friesian types even if cited in the (re-)validating diagnosis, if this diagnosis is in contradiction to the pre Friesian concept. There is only one complication which, by the tacit consensus of those concerned, has thus far been handled in a way suggesting the existence of an explanatory note supplementing Art. 20 saying that « transfers made after the starting data in the different groups (or : in « Fungi caeteri ») but regarding pre-Friesian names revalidated in the sense of a post Friesian author must be understood as transfers of the unit concerned in the post Friesian concept rather than in the original pre-Friesian concept, unless the transferring author makes a definite statement excluding the Friesian or post-Friesian concept such as « non Fries », and « nec Fries » [19]. Since such a note does not exist at present, it would appear that there is a definite need for it, and it should rather be accepted before the first differences of interpretation break out into monographs than afterwards. The nomenclatorial problems in which this tentative provision

[18] *International Rules of Botanical Nomenclature adopted at the International Botanical Congresses of Vienna, Brussels... Cambridge*, Jena, 1935.

[19] *Example :* Gray's description of *Leccinum scabrum* goes back to some author that probably had a species in view that is not identical with *Boletus scaber* Bull. or *Boletus scaber* Fr. However, since he does not explicitly exclude Fries's concept, *Boletus scaber* Bull. ex Fr. can be correctly transferred to *Leccinum* under the binomial *Leccinum scabrum* (Bull. ex Fr.) S. F. Gray. Without a note of explanation as suggested above, Gray's name would not be valid for the Friesian *B. scaber* since it does not refer to Fries. When the Friesian species is transferred to *Leccinum*, this would not be possible under the epithet *scabrum* because by now *Leccinum scabrum* would be a homonym of Gray's binomial. As a result, two « nomina nova » would be necessary. Under the provision of the explanatory note, however, only one new name would be necessary, and even that new name has been taken care of by the publication of other binomials which were intended to designate new species rather than to become « nomina nova ».

may apply have been treated as if this provision were part of the rules.

Another particularly difficult problem is the application of the International Rules to sectional names. It is not only necessary to investigate the author's intention as to whether the group-name was actually meant to be a section (which was, in spite of superficial appearance, not the case with Burlingham's groups in *Russula* and *Lactarius*), or its equivalent. A named group beneath a section is usually interpreted as a subsection unless there is evidence to the contrary. Unspecified names (Latin adjectives in plural) below the subsection level, as are often proposed by Bataille, Lange, and others, are not accepted as prior to names with definite rank. The type of the sections and subsections is usually the species after which it is called, and for which it was primarily intended. If there is a discrepancy between the description and the correct interpretation of the type species, or if the sectional or subsectional name is not formed after a typical species the difficulties are often considerable. In such cases a tentative selection of a lectotype has been made with due consideration of the nomenclatorial changes involved with each alternative selection, and with a view of not causing unnecessary innovations in sectional and subsectional names. The range of units between species and order has thus far, from a nomenclatorial point of view, been treated in a very careless way by most authors. Yet, it appears that there should be no exception to the application of the general principles of nomenclature, even in those units that do not immediately influence the binomial nomenclature of the species.

Some of the names of families, initially accepted or even proposed by the author himself, appear to be in disaccord with the pertinent rules governing the naming of families (Art. 23), and had to be changed accordingly. In other cases, the type concept was involved when certain genera were transferred into other families, and the name of the family had to be changed even though the larger number of genera and species belongs to the family whose name must disappear. Family names that were proposed at a time when the rules for the formation of family names were not yet formulated, and were, accordingly, not given the correct ending (in *aceae*), are generally admitted as validly published, and the corresponding change in the ending is made, wherever necessary, in the same way as this appears to be admissible in the case of incorrectly formed specific names (consisting of two words, misspelled, etc.). This goes mainly for the

families that have been proposed by Roze (1876) who gave a description of each of them in a subsequent paper, indicating several genera belonging in each of the families. On the other hand, the family names proposed by van Overeem in his later papers, cannot be considered as validly published since they have no description accompanying the names which are consequently «nomina nuda». All these considerations made it necessary to abandon the family name *Leucocoprinaceae* in favor of *Agaricaceae*, and *Rhodogoniosporaceae* in favor of *Rhodophyllaceae*.

Generally, it is felt that, if ever, nomenclature must be brought into accordance with the rules — now. There are so many changes in the taxonomic field that a few additional changes on the basis of legality will pass almost unnoticed. In the opinion of the majority of those concerned with issues of nomenclatorial order, it is bad policy to keep inconvenient but legal names in the dark, hoping that nobody will discover them. They will eventually be brought to light, and this will be at a time when the consequences will be felt much more severely. It is true that these consequences can then be corrected by conservation. But it is the general consensus that conservations should be kept at a minimum, and, besides, there is in the Rules no provision made for the conservation of specific names — and there should not be.

SPECIAL PART

THE FAMILIES, GENERA, AND SPECIES OF THE «AGARICALES» IN SYSTEMATIC ARRANGEMENT

Order: AGARICALES Clements

Genera of Fungi, p. 102, 1909; sensu str. *Rea, Brit. Bas.*, p. xi, 1922.

This order was first proposed in the *North American Flora* in parentheses, and without a diagnosis, but the meaning was the same as in Clements's survey, i. e. a valid order name for what was then called the *Hymenomycetes*. Since the word *Agaricales* in itself indicates the type family (*Agaricaceae*) and the type genus (*Agaricus*), it is obvious that we have to use it for the order containing the genus *Agaricus* and the family *Agaricaceae*, i. e. for the order which we are treating in this book. However, it appears that in their old delimitation neither *Hymenomycetes* nor *Agaricales* were acceptable.

It has been shown before that the division of the homobasidial *Basidiomycetes* into *Gastromycetes* and *Hymenomycetes* is arbitrary, and some may find it preferable to divide the *Eu-Hymeniales* R. Maire ex Lotsy, em. in *Gymnocarpi* (Pers. ex) Pat. and *Gastropileati* Bond. & Sing. (*nom. nud.*) as was (*ad int.*) suggested in a recent paper [50]) as a counterproposal. The word *Agaricales*, still used as an order, was later emended to contain all of Clements's *Agaricales* minus the *Gasteromycetales* and *Aphyllophorales* of Rea's classification. This is the sense in which it is used here, and this is also the way it is used by most modern taxonomists as far as they are independent specialists (Konrad & Maublanc; R. Maire, etc.) of this group. Only a few have gone one step farther. They distinguish two smaller orders from the remainder of the *Agaricales*, i. e. the *Boletales* (Gilbert), the *Asterosporales* (or Asterospores) of Malençon, and the *Agaricales* sensu str. The author believes that the distinction of an autonomous order *Boletales* is at least premature. In fact, the *Boletales* are undoubtedly closely related to certain families of *Agaricales*, and even the compromise solution of subdividing the *Agaricales* into two suborders *Boletineae* Rea and *Agaricineae* auct. as accepted by the author in 1936 does not express the real affinities. There is no necessity at present to distinguish suborders. The order *Asterosporales*, meant to contain the *Russulaceae* and the corresponding gastromycetoid family called *Astrogastraceae* by Malençon and Heim, appears to be much more justified than the order *Boletales*. There is no close affinity between the *Russulaceae* and the remaining families of the *Agaricales*, at least not as close an affinity as observed between the remaining families. On the other hand, it may be preferable to be somewhat hesitant in piecing together gastromycetoid families and agaricoid families to « mixed » units of a higher taxonomic level at the present time. While there is no doubt about the actual affinity of the two families in question, — there is also no doubt about other « mixed » groups such as *Rhizopogonaceae* plus *Boletaceae-Strobilomycetaceae*; though in this case, it would be extremely difficult to define the limits of the groups obtained — it is a half hearted [51] and inconsistent solution to single out the *Asterospo-*

[50] BONDARZEW, A. & R. SINGER, *Zur Systematik der* Polyporaceae, *Ann. Myc*, **39**: 43, 1941.

[51] As soon as it will be possible to delimit « mixed groups » of this order, we shall see the *Agaricales* fall apart, the fragments being: 1. *Asterosporales* (or rather the valid name *Russulales*), 2. *Boletales* sensu lato (including *Rhizopogo-*

rales merely on the grounds that they are easier to delimit. At the present time, the *Russulaceae* are still generally considered as part of the «agarics», i. e. representatives of the order *Agaricales*, and while admitting their relative isolation, the author does not at present separate them nomenclatorially (as in contrast to phylogenetically) from the bulk of the *Agaricales*.

A slight emendation in the sense of the order *Agaricales* has also been made on behalf of certain isolated genera that have thus far been considered as belonging to the *Cyphellineae*, «Thelephoraceae», *Clavariaceae*, etc. These are in the opinion of the author as well as of others (Patouillard, Romagnesi, Donk, Krieger) nothing but representatives of the family *Tricholomataceae*, especially of the tribes *Hemimyceneae* and *Myceneae* [33]. Since at least some of them seem to be perfectly gymnocarpous and lacking any trace of lamellae or pores, it is hard to shortly summarize the difference between these groups and the corresponding aphyllophoraceous groups. However, the decisive reasons for their addition to the *Agaricales* are these:

1. Presence of hairs on the sterile surfaces that are almost perfectly like those of tricholomataceus genera such as *Marasmiellus, Chaetocalathus*, etc., or of dermatocystidia that correspond to those in the *Tricholomataceae*.

2. The similarity in appearance and development between the astipitate species of *Chaetocalathus* and certain agaricoid *Cyphellae* on one hand, and between certain irregularly pileate species of *Marasmiellus* and the species of *Physalacria* on the other hand.

3. The fact that in some undoubtedly agaricoid species of *Mycena, Marasmiellus* and *Marasmius*, the hymenophore is absent in certain populations or individual carpophores, especially the young (but already sporulating) ones, and the fact that genera without a differ-

naceae, etc.), 3. An order containing the family *Amanitaceae*, 4. *Agaricales* sensu strictissimo (*Agaricaceae, Bolbitiaceae, Coprinaceae*, etc. plus *Secotiaceae, Montagnea*, etc.) and perhaps a group for *Crepidotaceae, Hygrophoraceae* and *Tricholomataceae* which may, however, rather be combined with either the group containing the *Amanitaceae*, or that containing the *Paxillaceae* which will probably be the *Boletales*. It is the author's firm conviction that this tentative «classification of the future» is definitely premature for all practical purposes.

[33] It is amazing how far convergence of characters in species with similar habit and habitat can go. Some species of *Dasyscypha* (*Discomycetes*) show remarkable similarities in external appearance, in marginal hairs and general structure.

cut ated hymenophore are found to be parallel to *Marasmius (Hymenogloea)* and *Marasmiellus (Cymatella)*.

4 All important anatomical and microchemical characters in the reduced forms and in the forms of *Tricholomataceae* to which they are supposed to be related, are identical. Among these are: pseudoamyloidity of the hairs: presence of clamp connections, epicutis of the pileus of the *Rameales* type (see genus *Marasmiellus*), and, valid for all of these forms, presence of basidioles of the *Collybia Marasmius* type (i. e. fusoid).

In spite of the difficulties arising from the various emendations of the limits of the *Agaricales*, a diagnosis embracing all forms considered as belonging in this group is attempted in the following paragraph:

Carpophores annual, never effuse resupinate at maturity but either stipitate pileate, or pileate with reduced stipe whereby the pileus assumes an ostreate or cupshaped appearance and sometimes develops a pseudostipe on the pileus (sterile side): 0.5 mm to 500 mm in diameter and 1 500 mm in height, membranous, or fleshy, or fleshy-tough, rarely almost leathery in consistency, and occasionally partly or entirely gelatinous, but never woody or carbonaceous; in most cases with a distinct and well developed hymenophore which is mostly lamellate, more rarely (but still often) tubulose (porous), and then the trama or the spores amyloid or the hymenophore more or less bilateral; very rarely venose or absent and in these cases with all anatomical characters in common with affine lamellate species or genera[33]. Species with pseudostipe are always thin, submembranous to flexible tough, or fleshy fragile, or partly gelatinous, never thick and corky tough; and their spores are often amyloid or pseudoamyloid, or the lamellae are longitudinally split, or the hairs of the sterile surface are pseudoamyloid, or beset with calcium oxalate crystals; volva sometimes present; marginal veil sometimes present; indusium sometimes present; pellicular veil or cortina sometimes present, pseudorhiza, or a sclerotium sometimes present.

Spores with evenly rounded outside, or nodulose, nodose stellate, angular, smooth or nodulose-rough, spinose, echinate, finely echinulate, warty, punctate, longitudinally ridged, or with a fragmentary or complete network (reticulate), with short interrupted ridges, or

[33] Hymenophore developing gymnocarpously, hemiangiocarpously, pseudoangiocarpously, very rarely angiocarpously

with warts connected with very fine anastomosing lines; isodiametric to strongly elongate, most frequently ellipsoid or slightly ovoid, also often subglobose or cylindric with rounded ends, or subfusoid to fusoid, with or without suprahilar depression or applanation, heterotropic and axillarly asymmetric (i. e. the geometrical axis at the lower end not touching the point of attachment of the hilar appendage), rarely subsymmetric, truncate at the upper end, especially when provided with a germ pore, or non-truncate; wall very thin (beyond the size of measurability by ocular micrometer and oil immersion lens), thin, somewhat thickened (0.5-1.0 µ), or thick, simple or compound, i. e. either stratose and consisting of an endo- and an episporium, or with imbedded heterogeneous ornamentations (mostly short spines), if stratose more often than not provided with a germ pore or a callus, exceptionally with 2-5 germ pores, amyloid, pseudoamyloid or nonamyloid, formed continuously during the life time of the carpophore, or, especially in reviving (light spored) carpophores, formed only during a short fertile period or several such periods. Aside from basidiospores, chlamydospores are sometimes formed in the hymenophore or in the surface of the pileus; oidia and conidia are occasionally formed, but not distinctive.

Basidia clavate or constricted to cylindrically attenuate above (false *Uniqura* type), (1-) 2- 3- 4-spored, always chiastic, with the third division usually taking place in the sterigmata before the entering of the (usually) four nuclei (resulting in the second division) into the four spores (whereby one of the resulting nuclei turns back into the basidium to degenerate. species with uninucleate spores), or with the third division taking place in the spores at their maturity (species with binucleate spores); with mostly half sickle-shaped sterigmata which are not strongly elongate; with or without a clamp between the last tramal or subhymenial cell and the basidium, with or more often without carminophilous granulosity, unicellular, in the immature stage (without sterigmata) either narrowly clavate or fusoid thin walled, rarely thick walled, sometimes regularly interrupted by pseudoparaphyses, or with interspersed cystidia of various types, or with pseudocystidia macrocystidia, gloeocystidia, etc.); the edge of the lamellae or pore walls often heteromorphous or almost heteromorphous, with cheilocystidia.

Trama more commonly than not consisting of both fundamental and connective tissue, frequently with oleiferous hyphae, laticiferous hyphae, and other elements of the conducting system; fundamental

tissue often consisting of sphaerocysts (*Russulaceae*), or of large elements, in the latter case these often coenobial (multinucleate), especially in the stipe; the hyphae sometimes slightly gelatinized with thick walls, or imbedded in a gelatinous mass and then usually thin-walled; amyloid or nonamyloid; hyphae with clamp connections or without them. Hymenophoral trama bilateral, inverse, regular, irregular, or intermixed Subhymenium present or more rarely absent, either ramose (filamentous), cellular, or intermixed. Hymenopodium either present, or more often absent.

Cortical layers of the pileus and the stipe either little differentiated, or dense, or forming a cutis, or a trichodermium, or a hymeniform layer, or an epithelium, often divided into two to rarely three layers, and sometimes covered by remainders of the velar layer: the outermost layer (mostly the epicutis) often containing dermatocystidia or dermatopseudocystidia, or hair like bodies; the walls of the hair-like bodies sometimes pseudoamyloid to amyloid; the walls of other epicuticular hyphae often gelatinized or imbedded in a gelatinous mass.

Mycelial tomentum present or almost absent at the base of the stipe and consisting of thin to moderately thick walled, filamentous, multiseptate or very long hyaline or colored hyphae. Mycelium filamentous, rarely forming sclerotia or pseudosclerotia, stilboids, or rhizomorphs, normally divided into two phases, the first resulting from the germination of the spores; the second from the copulation of two hyphae of the haploid mycelium.

Parasitic on the roots of trees, on the roots of herbaceous plants, shrubs, etc., also on trunks of trees, on stems of herbaceous plants and shrubs, even on twigs and leaves of living plants or their fruits; also saprophytically on all kinds of plant debris (even animal debris such as bones, hair), often very specialized as to species and organ of the host, also on dung, also on thinly scattered organic matter on sand, rocks, on living trees, pavement, etc., or on the naked earth in pastures, meadows, steppes, tundras, deserts, gardens, roadsides, greenhouses, cellars, often on various artificial matter such as some plastics, sawdust, wooden structures, putty, charcoal heaps, ropes, clothing, etc.: or in close connection with stands of mosses such as *Sphagnum*, *Polytrichum*, etc., or *Pteridophyta* such as *Pteris*, *Osmunda*, etc.; or in symbiosis with *Coniferae* (mycorrhiza ectotrophic), *Dicotyledones* (mycorrhiza ectotrophic), or *Monocotyledones* (orchids; mycorrhiza endotrophic), but never in symbiosis with *Algae* (i. e.

never lichenized). In all zones and continents, altitudes and plant societies, but never truly aquatic. Life cycle never truly dioecic as far as known, but sometimes with a leaf-parasitic or twig parasitic phase on a definite host plant, and a saprophytic, sexual phase on forest humus. Fruiting periods mostly highly seasonal in the boreal and in the temperate as well as in the tropical zones.

KEY TO THE FAMILIES

A. Trama of the pileus and stipe homoiomerous; non amyloid or amyloid; spore with or without an amyloid exosporial ornamentation; hyphae with or without clamp connections

B. Trama of the hymenophore bilateral, with a lateral layer of diverging hyphae; this outer layer or the mediostratum sometimes reduced, and then a strongly developed, irregular to intermixed hymenopodium present and the lamellae either thick and obtuse, or strongly forked

C. Hymenophore lamellate, lamellae more or less decurrent, often rather distant, thick and waxy; pileus often viscid or glutinous; spore print white; spores smooth, non-amyloid; numerous clamp connections; basidia abnormally long (about six times as long as the spore length in an average). **Hygrophoraceae**, p. p. (p. 141)

C Fungi never combining the characters indicated above

D. Lamellae deeply decurrent to adnexed, not free; spores anucleate, amyloid, veil well developed, sometimes double **Tricholomataceae** (*Biannularieae*) (p. 155

D Not combining the above characters.

E. Hymenophore lamellate

F Hymenophore free or almost so; trama often with isolated elements of the fundamental tissue; spores often amyloid, mostly white, more rarely cream color, pink or greenish in print; veil often well developed **Amanitaceae** (p. 577

F. Hymenophore not free, usually decurrent; trama never with isolated elements of the fundamental tissue, spores never amyloid, rarely pure white or cream color in print, usually between « chamois » and deeper brown, deep olive or black; veil well developed or none

G. Clamp connections present, **Paxillaceae** (p. 624) (mostly)

1. Spores completely hyaline under oil immersion lens, smooth and not angular in any view; lamellae not repeatedly forked; or: spores not quite hyaline and thick walled, not always quite smooth but never angular, and then lamellae with strong concentric anastomoses, more rarely without them, and basidia with rather thick walls. (see *Tricholomataceae*)

1. Not so

2. Spores more or less brownish under the microscope, smooth or not;

KOH and NH_4OH almost negative with all parts of the carpophore; lamellae usually distinct and simple; coscinoids none. (see *Crepidotaceae*)

2. Spores or reactions not as above; lamellae usually more or less anastomosing, or coscinoids present.
   3. NH_4OH not blue on cuticle. *Paxillaceae*
   3. NH_4OH bright blue on fresh cuticle of pileus. (see *Boletaceae*)

G. Clamp connections absent

Gomphidiaceae (p. 634) (mostly)

1. Spores deep rustbrown to usually almost black in print; lamellae rather thick and often obtuse at the edge, rather distant; cystidia present, scattered to numerous, usually voluminous and elongate; mycorrhiza constantly with conifers. *Gomphidiaceae*
1. Not combining the above characters.
   2. Spore print deep olive. (see *Strobilomycetaceae* and *Boletaceae*)
   2. Spore print « chamois » or deeper brown (not nearly black), or some shade of sordid pink. (cf. *Rhodophyllaceae* and *Paxillaceae*)

E. Hymenophore tubulose

H. Spores with some kind of ornamentation.

Strobilomycetaceae (p. 688) (mostly)

1. Cystidia prominent; basidia thin walled; concentric hymenophoral walls of equal height. *Strobilomycetaceae*
1. Cystidia not prominent, basidia rather thick walled; concentric hymenophoral walls much lower than the radiating walls (lamellae) or even indistinct. (see *Tricholomataceae*)

H. Spores without any ornamentation.

Boletaceae (p. 641) (mostly)

1. Spore print « warm sepia », « hazel » (Ridgway), or black. (see *Strobilomycetaceae*)
1. Spore print some other color.
   2. Spore print with an olivaceous tinge.
      3. Spores broadly fusoid, with suprahilar depression, strongly colored (deep melleous to light castaut, or sepia under the microscope), with an incomplete germ pore or with acuminate apex, with rather thick (1 µ or thicker in completely mature spores) wall; hyphae always without clamp connections, hymenophore always strongly ventricose, stipe never ventricose-bulbous; hymenial elements usually comparatively voluminous (see *Strobilomycetaceae*)
      3. Not combining all these characters. *Boletaceae*
   2. Spore print without an olivaceous tinge. *Boletaceae*

B. Trama not bilateral; hymenopodium, if present, consisting of parallel or subparallel hyphae.

I. Trama of the hymenophore inverse; spore print pink; spores stramineous under the microscope; lamellae free, thin

Amanitaceae (p. 377) (*Pluteeae*)

I. Trama of the hymenophore not inverse; spore print pink or some other color; spores stramineous or some other color; lamellae free or not, thin or thick

J. Spores angular from whatever side they are observed, or angu-

lar only from an end view (longitudinal axis pointing to the objective), with the longitudinal sides of the spores either rough (finely warted) or not ornamented, spore walls never amyloid; spore print pink. **Rhodophyllaceae** (p. 601)

J. Not combining these characters.

K. Spores pseudoamyloid, but pseudoamyloid epicuticular elements absent; lamellae free; annular veil or velar floccons usually present. **Agaricaceae** p. p. (p. 406)

K. Spores and lamellae not as above.

L. Spore print pure white; spores nonamyloid with thin walls; hyphae with numerous clamp connections; basidia long in relation to the length of the spores (about 5.5-7 times as long as the spores); lamellae (because of the thick hymenial layer) rather thick and of a waxy consistency, never free; pileus and stipe often viscid; cystidia on the side of the lamellae none, or inconspicuous; pigment of the whole carpophore often a very bright red or yellow.

Hygrophoraceae p. p. (p. 141) (mostly).

1. Veil present, or with a hymeniform epicutis, or with diverticulate hyphae forming an epicutis. (see *Tricholomataceae*)

1. Veil none, without a hymeniform epicutis, or with a somewhat hymeniform epicutis in which the elements are loosely arranged and imbedded in a gelatinous mass; diverticulate hyphae none *Hygrophoraceae*

L. Not combining the above characters.

M. Spore print pure white, cream color, pale pink to light brownish pink, green, purplish-rose color, or a pale drab, spores never with a germ pore, more often uninucleate than binucleate.

Tricholomataceae p. p. (p. 155) (mostly)

1. Lamellae decurrent, repeatedly forked; spores small, smooth, nonamyloid; trama rather soft as in the boletes, nonamyloid; hyphae with clamp connections. (see *Paxillaceae*)

1. Not combining these characters

2. Lamellae free; veil present; cuticle with sphaerocysts or hymeniform. (see *Agaricaceae*)

2. Not combining these characters.

3. Pileus and stipe, or very rarely stipe alone, covered with a mealy or furfuraceous coating that consists mainly of sphaerocysts; veil present; spores usually small, rarely medium (around 10 μ), nonamyloid or amyloid or weakly pseudoamyloid, smooth, white or whitish in print. (see *Agaricaceae*)

3. Not combining these characters.

4. Spores pink or sordid pink with moderately thin wall; basidia rather voluminous; clamp connections usually none; veil none; characters in general similar to those of certain species with angular spores. (cf. *Rhodophyllaceae*)

4. Not combining these characters.

5. Stipe with a marginate bulb; veil cortinoid; spore print cream color (see *Cortinariaceae*)
5. Not combining these characters.
6. Spore print russet pink or purplish pink; epicutis cellular; spores with germ pore which may occasionally be indistinct (see *Coprinaceae*)
6. Not combining these characters
7. Pileus woolly-scaly; lamellae completely free; spores amyloid; veil distinct (see *Agaricaceae*)
7. Not combining these characters
8. Cortina present; spore wall with an episporium and an endosporium, pale stramineous under the microscope; thick-walled cystidia present. (see *Cortinariaceae*)
8. Not combining these characters.
9. Basidia six times as long as the spores or longer; lamellae decurrent, distant, not repeatedly forked, thick; veil none; clamp connections present; hymenophoral trama intermixed irregular; cystidia none of any kind; cuticle dense, glabrous. (see *Hygrophoraceae*)
9. Not combining these characters.
10. Spores small, rough, nonamyloid; cystidioles characteristic, shaped as in *Melanoleuca* (with crystalline capitellum); veil present; clamp connections present; habit of the carpophores as in *Lepiota*. (see *Agaricaceae*)
10. Not combining these characters.
Tricholomataceae

M. Spore print argillaceous, melleous, ochraceous to chamois, ochraceous brownish, cinnamon, bright rusty, rusty brown, ferruginous fuscous, purplish fuscous, deep fuscous to black, cinnamon brown, deep lilac to blackish lilac; spores mostly binucleate at the time of discharge
N. Spores with germ pore, with or without truncate apex.
O. Hymenophore of the inaequihymeniiferous type; spores deep fuscous or black.
Coprinaceae p. p. (p. 452).
O. Not combining these characters.
P. Epicutis consisting of filamentous, repent hyphae.
Q. Lamellae free; volva or annular veil, or both, usually present; spore print purplish brown (warm

sepia); spores ellipsoid or ovoid, or subglobose, smooth; cheilocystidia absent or rather inconspicuous, vesiculose or catenulate, or in the contrary very voluminous but then very variable and fugacious; basidia small; cystidia usually none, chrysocystidia never present.

Agaricaceae p. p. (p. 406).

Q. Lamellae subfree to decurrent; annulus present or absent; volva none; spore print purplish brown, or some other color; cheilocystidia usually present and well developed, usually making the edge of the lamellae more or less heteromorphous or subheteromorphous; basidia rather small to rather large, sometimes very broad and voluminous; cystidia absent, or present, and in the latter case mostly representing the type « chrysocystidia »

Strophariaceae (p. 495) (mostly).

1. Context rather dry and somewhat tough; growing in arid regions on the ground; pileus globose to cylindric or long-fusoid, opening late, after maturity with longitudinal cracks, never expanding; spores in NH_4OH melleous or bright rusty ochraceous (see *Bolbitiaceae*

1. Not combining these characters. *Strophariaceae* (but cf. *Bolbitiaceae*, if spores are warty).

P. Epicutis hymeniform, or a hymenium, or an epithelium

R. Spore print bright rusty to deep ferruginous, or ferruginous-fuscous, or argillaceous brown (without a purplish tinge).

Bolbitiaceae p. 475).

R. Spore print purplish fuscous, deep fuscous to black, or rarely russet pink or purplish rose color, discolored to livid grayish in H_2SO_4, or black or deep purplish fuscous and remaining so in H_2SO_4

Coprinaceae p. p (p. 452) (mostly).

1. Lamellae free or subfree; spores ± sulangular or nodulose when seen in profile; cheilocystidia catenulate; volva none. (see *Agaricaceae*)

1. Lamellae subfree to subdecurrent ; spores subangular or with oval, elliptical, cylindrical, etc. outline, sometimes warty, never nodulose ; cheilocystidia always conspicuous but not catenulate ; volva present or absent. *Coprinaceae*

N. Spores without a germ pore

S. Spores neither bright rusty in print nor with a plage, nor with a superficial ornamentation (warty), nor nodulose ; cuticle neither hymeniform nor in palisade, nor cellular, nor darkening to black when treated with alkalis ; veil present or absent but rarely truly cortinoid ; conspicuous metuloids never present.

Crepidotaceae (p. 584) (mostly).

1. Spores melleous ; stipe central ; veil often present ; cuticle more or less viscid to glutinous ; cheilocystidia conspicuous.
   2. Spores fuscous ferrugineous in print (see *Strophariaceae*)
   2. Spores sordid argillaceous brown in print (see *Cortinariaceae*)
1. Not combining these characters
   3. Stipe eccentric or lateral, or almost absent.
      4. Bright yellow pigment, easily dissolving in NH_4OH present ; spores smooth, with double wall, rather deep colored ; cheilocystidia very prominent ; hyphae with clamp connections (see *Strophariaceae*)
      4. Not combining these characters. *Crepidotaceae*
   3. Stipe central.
      5. Pileus radiately fibrillose or rimose or squarrulose ; spores with double wall and smooth, not pale brownish but well colored under the microscope, not collapsing easily ; odor not raphanaceous. (see *Cortinariaceae*)
      5. Not combining the above characters.
         6. Spore and basidium wall rather thick ; habit mycenoid or collybioid ; lamellae intervenose. (see *Tricholomataceae*)
         6. Not combining these characters. *Crepidotaceae*

S. Spores brightest rusty in print, or with superficial warty ornamentation, or with a plage, or nodulose — or with an even outline and not bright rusty in print, and without a superficial warty ornamentation and without a plage, but then either with a hymeniform or palisadic epicutis, or with epithelium or darkening with alkalis, or with truly cortinoid veil, or with characteristic metuloids.

Cortinariaceae (p. 522) (mostly).

1. Habit pleurotoid ; spore print not bright rusty (see *Crepidotaceae*)
1. Not combining all these characters.
   2. Chrysocystidia present. (see *Strophariaceae*)
   2. Chrysocystidia none

3 Epicutis cellular and spores in mass purplish fuscous to black
(see under « O »)

3 Epicutis cellular, or not; spores in mass never with a purplish tinge, or nearly black. *Cortinariaceae*

A Trama of the pileus and stipe heteromerous, nonamyloid; spores always with an exosporial ornamentation that is amyloid; hyphae always without clamp connections. Lamellae often all equal and at the same time numerous; latex often present in the carpophores **Russulaceae** p. 697.

SURVEY OF THE FAMILIES AND GENERA OF THE « AGARICALES »

Family 1. **HYGROPHORACEAE**

Genera: 1. *Hygrophorus*, 2. *Camarophyllus*, 3. *Neohygrophorus*, 4. *Hygrocybe*, 5. *Bertrandia*.

Family 2. **TRICHOLOMATACEAE**

Tribus: **Lyophylleae**

Genera: 6. *Lyophyllum*, 7. *Calocybe*, 8. *Asterophora*.

Tribus: **Clitocybeae**

Subtribus: *Clitocybinae*

Genera: 9. *Laccaria*, 10. *Lampteromyces*, 11. *Hypsizygus*, 12. *Omphalotus*, 13. *Clitocybe*, 14. *Lepista*, 15. *Tricholomopsis*, 16. *Collybia*, 17. *Pleurocybella*, 18. *Nothopanus*, 19. *Anthracophyllum*, 20. *Trogia*.

Subtribus: *Tricholomatinae*

Genera: 21. *Omphalina*, 22. *Armillariella*, 23. *Tricholoma*, 24. *Podabrella*, 25. *Pleurocollybia*, 26. *Callistosporium*.

Tribus: **Leucopaxilleae**

Genera: 27. *Cantharellula*, 28. *Leucopaxillus*, 29. *Lentinellus*, 30. *Melanoleuca*.

Tribus: **Resupinateae**

Genera: 31. *Resupinatus*, 32. *Hohenbuehelia*.

Tribus: **Panelleae**

Genera: 33. *Panellus*, 34. *Dictyopanus*.

Tribus: **Schizophylleae**

Genus: 35. *Schizophyllum*

Tribus: **Lentineae**

Genera: 36. *Tectella*, 37. *Phyllotopsis*, 38. *Pleurotus*, 39. *Panus*, 40. *Lentinus*, 41. *Geopetalum*, 42. *Asterotus*.

Tribus: **Hemimyceneae**

Genera: 43. *Oudemansiella*, 44. *Xerula*, 45. *Mycenella*, 46. *Marasmiellus*, 47. *Micromphale*, 48. *Flammulina*, 49. *Macrocystidia*, 50. *Phaeomycena*, 51. *Lactocollybia*. Reduced

series: 52. *Cymatella*, 53. *Flagelloscypha*, 54. *Physalacria*

Tribus: **Myceneae**

Subtribus: *Marasmiinae*

Genera: 55. *Pseudobaeospora* [sic?]

Tribus: **Biannularieae**

Genera: 71. *Catathelasma*, 72. *Armillaria*.

Family 3. AMANITACEAE

Tribus: **Amaniteae**

Genera: 73. *Amanita*, 74. *Limacella*, 75. *Termitomyces*, 76. *Rhodotus*

Tribus: **Pluteeae**

Genera. 77. *Volvariella*, 78. *Chamaeota*, 79. *Pluteus*

Family 4. AGARICACEAE

Tribus: **Leucocoprineae**

Genera: 80. *Clarkeinda*, 81. *Chlorophyllum*, 82. *Macrolepiota*, 83. *Leucoagaricus*, 84. *Leucocoprinus*.

Tribus: **Agariceae**

Genera: 85. *Agaricus*, 86. *Cystoagaricus*, 87. *Melanophyllum*.

Tribus: **Lepioteae**

Genera: 88. *Pseudobaeospora*, 89. *Lepiota*.

Tribus: **Cystodermateae**

Genera: 90. *Drosella*, 91. *Smithiomyces*, 92. *Cystoderma*, 93. *Phaeolepiota*, 94. *Ripartitella*.

Family 5. COPRINACEAE

Subfamily: *Coprinoideae*

Genera: 95. *Xerocoprinus*, 96. *Coprinus*.

Subfamily: *Psathyrelloideae*

Genera: 97. *Pseudocoprinus*, 98. *Macrometrula*, 99. *Psathyrella*.

Subfamily: *Panaeoloideae*

Genera: 100. *Panaeolina*, 101. *Panaeolus*, 102. *Copelandia*, 103. *Anellaria*.

Family 6. BOLBITIACEAE

Genera: 104. *Cottarophyllum* [sic?], 105. *Conocybe*, 106. *Galerella*, 107. *Pholiotina*, 108. *Tubariopsis*, 109. *Bolbitius*, 110. *Agrocybe*.

Family 7. **STROPHARIACEAE**

Subfamily: *Strophariοideae*

Genera: 111. *Stropharia*, 112. *Naematoloma*, 113. *Psilocybe*, 114. *Deconica*, 115. *Melanotus*.

Subfamily: *Pholiotoideae*

Genera: 116. *Pholiota*, 117. *Kuehneromyces*, 118. *Pleuroflammula*.

Family 8. **CORTINARIACEAE**

Tribus: **Inocybeae**

Genera: 119. *Inocybe*, 120. *Hebeloma*, 121. *Alnicola*, 122. *Naucoria*.

Tribus: **Cortinarieae**

Genera: 123. *Rozites*, 124. *Cortinarius*, 125. *Leucocortinarius*, 125a. *Descolea*, 126. *Gymnopilus*, 127. *Phaeocollybia*, 128. *Pyrrhoglossum*, 129. *Galerina*, 130. *Phaeomarasmius*.

Family 9. **CREPIDOTACEAE**

Genera: 131. *Tubaria*, 132. *Ripartites*, 133. *Crepidotus*, 134. *Pleurotellus*.

Family 10. **RHODOPHYLLACEAE**

Genera: 135. *Clitopilus*, 136. *Rhodocybe*, 137. *Rhodophyllus*.

Family 11. **PAXILLACEAE**

Genera: 138. *Hygrophoropsis*, 139. *Paxillus*, 140. *Linderomyces*, 141. *Neopaxillus*.

Family 12. **GOMPHIDIACEAE**

Genera: 142. *Cystogomphus*, 143. *Gomphidius*.

Family 13. **BOLETACEAE**

Subfamily: *Gyrodontoideae*

Genera: 144. *Gyroporus*, 145. *Phaeogyroporus*, 146. *Paragyrodon*, 147. *Gyrodon*.

Subfamily: *Suilloideae*

Genera: 148. *Psiloboletinus*, 149. *Boletinus*, 150. *Suillus*.

Subfamily: *Xerocomoideae*

Genera: 151. *Phylloporus*, 152. *Xerocomus*.

Subfamily: *Boletoideae*

Genera: 153. *Phlebopus*, 154. *Pulveroboletus*, 155. *Boletus*, 156. *Xanthoconium*, 157. *Tylopilus*, 158. *Leccinum*.

Family 14. **STROBILOMYCETACEAE**

Genera: 159. *Strobilomyces*, 160. *Porphyrellus*, 161. *Boletellus*.

Family 15. **RUSSULACEAE**

Genera: 162. *Russula*, 163. *Lactarius*.

HYGROPHORACEAE Roze

(ut Hygrophorées) *Bull. Soc. Bot. Fr.* **23**: 51, 1876, nom. nud.; *ibid.*, p. 110, 1876; R. Maire, (ut Hygrophoracées) *Bull. Soc. Myc. Fr.*, Tabl. 1901, nom. nud.; *Rech. cyt. et tax. sur les Basidiomycetes*, Paris p. 114, 1902; Lotsy, *Vortr. Bot. Stammesgesch.*, p. 706, 1907.

Type genus : Hygrophorus Fr., *Gen. Hym.*, p. 8, 1836.

Characters : Pileus often viscid to glutinous, the cuticle consisting of radiately arranged, filamentous hyphae, often dense, more rarely consisting of repent or erect hyphae which are imbedded in a gelatinous mass; hymenophore lamellate; lamellae waxy and thick (not obtuse unless they are so because of a glutinous layer at the edge) because of the unusual length of the basidia (5,5-7 times as long as the spores); basidioles filamentous; sterigmata four, or two; spores thin-walled, small and globose to voluminous and cylindric, most frequently rather inconstant in size and shape and approximately ovoid-ellipsoid (-cylindric), always smooth, nonamyloid, rarely amyloid (and then lamellae distant, purplish drab, and decurrent; veil none; hymenophoral trama intermixed-irregular, red in KOH); cystidia none, or rather inconspicuous; basidia without carminophilous granulation; hymenophoral trama irregular to intermixed, or regular, or bilateral; stipe subcartilaginous to fleshy, sometimes viscid or glutinous, sometimes veiled, smooth or furfuraceous-fibrillose at the apex or longitudinally striate-fibrillose all over (the veiled forms always with bilateral hymenophoral trama); context mild or sometimes bitter, not acrid, usually fleshy in consistency at least in the pileus; hyphae always nonamyloid, always with numerous clamp connections; trama homoiomerous without separation-zones and never horny or chordaceous. On the ground in woods (mycorrhizal only in *Hygrophorus*), among mosses (frequently among *Sphagnum*), more rarely on decayed wood, charcoal.

Limits : This family cannot be based on the size of the basidia, or the thickness of the lamellae alone. There are other white-spored groups with the basidia as long as in the Hygrocybes, yet definitely not related to them; and there are other groups with thick lamellae (*Laccaria*), also not related to the *Hygrophoraceae*. In the latter, the spores are often echinate, and the basidia are less than 5,5 times longer than the spores. In the former, the clamps are lacking at all septa, and the affinities of these species are rather with the *Tricholo-*

mataceae (*Armillariella*, *Tricholoma*). These species also differ in the chemical reactions (generally reacting more actively), and do not fit into any of the sections established in *Hygrocybe*. They were considered as *Hygrophori* only because of the bright colors that may remind one in a certain way of *Hygrocybe*. But it appears that these pigments are neither colorimetrically nor chemically identical with those found in *Hygrocybe*.

The genus *Hygrophorus* may come close to *Clitocybe*. In some species of *Clitocybe* a rather distinct divergence of the almost regular hymenophoral trama in its outer regions can be observed, and then, the tramal structure may be considered as somewhat transitory. In this case, the viscidity of the pileus, a character rare in *Clitocybe*, the relative size of the basidia, the presence or absence of a veil (no veil in *Clitocybe*) will decide. In general, the distinction is very easy, even to the beginner, or at least becomes evident after some experience. The delimitation of *Clitocybe* and *Hygrophorus* does not represent a taxonomic problem. *Hygrophorus russula* has often been considered as a *Tricholoma* but without the slightest justification.

The genus *Gomphidius* has been considered as belonging in this family by some mycologists, or has at least been considered as closely related because of the thick waxy lamellae and the long basidia. However, the absence of clamp connections, the deep colored spores, the cystidia of the bolete type, the chemical reactions, and many other characters [44] show that the *Gomphidiaceae* are closer to the *Boletaceae* than to the *Hygrophoraceae*.

The tribus *Biannularieae* of the *Tricholomataceae* also has bilateral trama. However, it also has a veil, amyloid spores, and close to crowded lamellae, a combination of characters that is foreign to the *Hygrophoraceae* proper.

The genus *Asterophora* which was considered by some as belonging to the *Hygrophoraceae* is distinguished by the carminophilous granulosity of its basidia. The same character can serve as a safe means of distinguishing between all *Lyophylleae* (*Tricholomataceae*) which tend to have rather long basidia at times, and the *Hygrophoraceae*.

Phylogeny: Hardly anything can be said about the origin of this family. On the other hand, it appears that most of the *Tricholoma-*

[44] See table on p. 55 in Singer, *System der Agaricales*, *Ann. Myc.* **40**. 1942.

taceae, if not all, are easy to be linked with the genera of the *Hygrophoraceae* as they are known now, or with theoretical forms (with combinations of *Hygrophoraceae* characters not occurring).

It is not impossible to derive the *Hygrophoraceae* from such lamellate forms of the boletaceous circle of affinities as *Hygrophoropsis*, *Rhodophyllus*. A more satisfactory solution of this problem may, however, be expected through further discoveries of species now incompletely known or forms still undescribed. The opposite direction of evolution, i. e. from the *Tricholomataceae* to the *Hygrophoraceae* can hardly be accepted since the large size of the basidia, the small number of lamellae and many other primitive characters of the *Hygrophoraceae* cannot be explained in this manner. It also appears that the ramification that seems to have taken place, starting from the *Hygrophoraceae*, (toward *Oudemansiella* —, toward *Tricholoma* —, toward *Clitocybe* —, toward *Catathelasma* —, toward *Cantharellula*, etc.) can not easily be reversed.

KEY TO THE GENERA

A. Hymenophoral trama bilateral; veil often present; mycelium often forming mycorrhiza; not observed in the tropics. — 1. *Hygrophorus*, p. 144

A. Hymenophoral trama not bilateral.

B. Spores amyloid. — 3. *Neohygrophorus*, p. 149

B. Spores nonamyloid.

C. Hymenophoral trama consisting of narrow hyphae (up to 7 µ in diameter) which are intricately interwoven, often to a degree to make them appear intermixed; lamellae always decurrent or subdecurrent and pileus and stipe devoid of bright pigments (red, yellow, green, orange) though sometimes orange fulvous, cinnamon, or sordid livid; latex none. — 2. *Camarophyllus*, p. 147

C. Hymenophoral trama subregular (i. e. the hyphae are not quite parallel but still show a recognizable axillar arrangement, and then they are — at least many of them — broader than 7 µ) or strictly regular; pigment often bright colored; latex sometimes present.

D. Latex absent; pseudocystidia none, cheilocystidia rarely present. — 4. *Hygrocybe*, p. 150

D. Latex present; pseudocystidia present, restricted to the edge of the lamellae (as cheilocystidia). — 5. *Bertrandia* p. 155

1. HYGROPHORUS Fr.

Genera Hymenomyc., p. 8, 1836, em. Karst

Type species: Hygrophorus eburneus (Bull. ex Fr.) Fr.

Syn. *Limacium* (Fr. ut tribus) Schroeter in Cohn, *Krypt. Fl. Schles., Pilze*, p. 530, 188,

Characters: Those of the family. Lamellae, adnate-subdecurrent to deeply decurrent; hymenophoral trama bilateral; veil often present; cystidia very rare, and then inconspicuous; pseudocystidia none; spores nonamyloid. Usually growing in the neighborhood of trees and forming mycorrhiza with various genera of *Cormophyta*.

Development of the carpophores: gymnocarpous in some species, hemiangiocarpous or pseudoangiocarpous in others (Kühner; hemiangiocarpous in *H. hypothejus* according to Reijnders.

Area: Circumpolar, boreal to almost subtropical, not observed in the tropics.

Limits. The limits between *Hygrophorus* and *Camarophyllus* have occupied the mycologists for many years. The question seems to be settled now with the acceptance of Fayod's anatomical delimitation by Lange, Kühner, Singer, and A. H. Smith & Hesler. A certain parallelism occurring in these two genera does not necessarily mean that they are congeneric. The difference between them on the anatomical basis is very strict, and the hiatus between them strong enough to consider these genera as distinct.

State of knowledge. Thanks to the efforts of many mycologists in Europe and A. H. Smith & Hesler in the United States, the species of *Hygrophorus* can be considered as rather well known. Below, 52 species are listed that undoubtedly belong here and are autonomous.

Practical importance: As mycorrhiza fungi, the *Hygrophori* seem to be rather selective (three of them occur with larch exclusively, many with conifers or with frondose trees exclusively, one perhaps exclusively with *Tilia*), few occur with both *Angiospermae* and *Gymnospermae*. Consequently, they are likely to become important in forestry. All species known are edible as far as they have been tested, and *H. marzuolus*, a spring species occurring in mountain forests of *Abies*, is often sold in the markets in the Alps.

SPECIES

Sect. 1. CANDIDI Bat. (1910). Pileus without pigment, or slightly pigmented (colored pale ochraceous or pale tan on the disc only), rarely becoming deeper colored when dried properly).

Type species : H. eburneus (Bull. ex Fr.) Fr.

Subsect. Chrysodontini Sing. (1943). Veil not gelatinous-glutinous (i. e. not consisting exclusively of a colorless glutinous mass) but floccose or almost cortinoid and dry.

Type species : H. chrysodon (Batsch ex Fr.) Fr.

H. chrysodon (Batsch. ex Fr.) Fr. and several other, somewhat imperfectly known species.

Subsect. Pallidini Smith & Hesler (1939). Veil absent and stipe dry to somewhat moist, and at times subviscid-slippery to the touch.

Type species : H. sordidus Peck.

H. subalpinus A. H. Smith; *H. sordidus* Peck; *H. subsordidus* Murr.; *H. Karstenii* Sacc. & Cub.; *H. albidus* Karst.; *H. pusillus* Peck, and probably also *H. penarius* Fr.

Subsect. Eburnei Bat. (1910) (*Albidi* Sm. & Hesl.). Stipe with a viscid veil, without a dry cortinoid veil, and without a zone of floccons at the apex forming a velar zone.

Type species : H. eburneus (Bull. ex Fr.) Fr.

H. ponderatus Britz. sensu Sm. & Hesl.; *H. gliocyclus* Fr.; *H. rubropunctus* Peck; *H. eburneus* (Bull. ex Fr.) Fr.; probably also *H. chrysaspis* Métrod.

Sect. 2. PUDORINI Bat. (ut subsectio, Konr. & Maubl. 1924-37). Pileus pink, pale pinkish tan, brownish rose, salmon color, pinkish buff, sometimes tending towards tawny, russet or cinnamon, or even as dark as clay color or tawny olive (both in the sense of Ridgway), Kaiser brown, cameo brown, etc. Stipe without a glutinous veil or coating.

Type species : H. pudorinus (Fr.) Fr.

Subsect. Erubescentes Sm. & Hesl. (1939). Lamellae with vinaceous purple or pink or testaceous tinge in age, or becoming maculate in these colors.

Type species : H. erubescens (Fr.) Fr.

H. purpurascens (A. & S. ex Fr.) Fr.; *H. russula* (Schaeff. ex Fr.) Quél.; *H. russuliformis* Murr.; *H. proximus* Krieger; *H. amarus* Sm. & Hesl.; *H. erubescens* (Fr.) Fr.; *H. Kauffmanii* Sm. & Hesl.; *H. nemoreus* (Lasch) Fr.

Subsect. **Fulvoincarnati** Sm. & Hesl. (1939). Lamellae white to cream color, occasionally flushed pale pink but usually not in the colors indicated for subsection *Erubescentes*, most frequently white or whitish and not spotted.

Type species: *H. pudorinus* (Fr.) Fr.

H. pudorinus (Fr.) Fr.; *H. fragrans* Murr. (if really different from *H. pudorinus*); *H. Queletii* Bres.; *H. pacificus* Sm. & Hesl.; *H. bakerensis* Sm. & Hesl.; *H. tennesseensis* Sm. & Hesl.; *H. laricinus* Peck; *H. subisabellinus* Sm. & Hesl.; *H. subrufescens* Peck; *H. roseibrunneus* Murr.; *H. arbustivus* Fr.

Sect. 3. **DISCOIDEI** (Bat. ut subsectio) Konr. & Maubl. (1924-37). (Subsect. *Lutei* Sm. & Hesl.; *Brunnei* Sm. & Hesl. 1939). Pileus yellow to red, orange, tawny, russet, or dark pinkish tan, sometimes with a flush of live mixed with the above colors, and sometimes fuscous but then the lamellae yellow; stipe more or less viscid, often with a purely glutinous veil.

Type species: *H. discoideus* (Pers. ex Fr.) Fr.

H. lucorum Kalchbr.; *H. speciosus* Peck; *H. hypothejus* (Fr.) Fr. [with var. *aureus* (Arrh. apud Fr.) Imler]; *H. subsalmonius* Sm. & Hesl.; *H. discoideus* (Pers. ex Fr.) Fr; *H. vernalis* A. H. Smith; *H. leucophaeus* (Scop. ex Fr.) Fr.; *H. Laurae* Morgan; *H. variicolor* Murr.

Sect. 4. **COLORATI** Bat. (1910), em. [*Olivaceoumbrini* (Bat. ut subsectio) Konr. & Maubl. (1924-37). *Limacium* sect. *Communia* Sing. 1943]. Pileus olivaceous to fuligineous, gray, grayish fuscous.

Type species: *H. olivaceoalbus* (Fr.) Fr.

Subsect. **Olivaceoumbrini** Bat. (1910). (*Euhygrophorus* subsect. *Fuliginei* Sm. & Hesl. 1939). Stipe with a viscid coating of velar origin that is more or less colorless and thoroughly glutinous.

Type species: *H. olivaceoalbus* (Fr.) Fr.

H. olivaceoalbus (Fr.) Fr. (also allied species; their relationship is not fully understood at present, at least, the authors do not fully agree as to their synonymy); *H. fuligineus* Frost in Peck; *H. paludosus* Peck; *H. olivaceonitens* (Sing.) Sing. (Limacium, Sing. 1943); *H. megasporus* Sm. & Hesl.; *H. occidentalis* Sm. & Hesl.; *H. limacinus* (Scop. ex Fr.) Fr.; *H. fuscoalbus* (Lasch) Fr.

Subsect. **Tephroleuci** Bat. (1910) (Sect. *Clitocyboides*, subsect. *Atrocinerei* Sm. & Hesl. 1939; *Limacium*, sect. *Communia* subsect. *Tephroleucini* Sing. 1943; *Camarophyllus*, sect. *Caprini* Bat. 1910; *Hygrophorus* sect. *Tephroleuci* and *Caprini* Konr. & Maubl. 1924-

37). Veil, if present, not completely glutinous, mostly absent and then the stipe dry, rarely subviscid and somewhat slippery to the touch.

Type species: *H. agathosmus* (Fr.) Fr.

H. agathosmus (Fr.) Fr.; *H. pustulatus* (Pers. ex Fr.) Fr.; *H. marzuolus* (Fr.) Bres.; *H. camarophyllus* (A. & S. ex Fr.) Dumée, Grandjean & R. Maire [Agaricus, Fr. 1821; Hygrophorus caprinus (Scop. ex Fr.) Fr.; Camarophyllus, Karst.; Limacium, Kühner]; *H. calophyllus* Karst. [H. camarophyllus var. calophyllus Karst., Konr. & Maubl.; H. caprinus var. calophyllus (Karst.) Quél.; Limacium calophyllum (Karst.) Sing.].

KEY TO THE SPECIES

Good keys — though not including the species of Eastern Asia — have been published recently and may be consulted (*Lloydia* 2: 4-7. 1939; *ibid.* 5: 82-84. 1942; *Ann. Mycol.* 41: 2-7. 1943).

2. CAMAROPHYLLUS (Fr.) Karst.

Bidr. Finl. Nat. Folk 32: xvii. 1879.

Type species: C. pratensis (Pers. ex Fr.) Karst.

Syn.: *Agaricus* trib. *Clitocybe* subtribus *Camarophyllus* Fr., *Syst. Mycol.* 1: 98. 1821.

Hygrophorus tribus *Camarophyllus* Fr., *Epicrisis* p. 325, 1838.

Characters: those of the family; pileus not very brightly colored, or buffy orange to almost orange, sometimes sordid livid, or white, viscid or dry; lamellae adnato-subdecurrent to decurrent, distant, not repeatedly forked; hymenophoral trama almost intermixed or at least so irregular that the axillar trend is hardly recognizable, consisting of hyphae with a diameter not larger than 7 μ; spores nonamyloid, uninucleate (according to Kühner); basidia not blackening with age, 4-spored, or 2-spored; cheilocystidia, pseudocystidia, cystidioles, etc. none; stipe colored much like the pileus or paler to white; veil none; context not reddening when exposed to the air, and when treated with KOH, without latex. In open woods, pastures, montane meadows, fields, lawns, more rarely (especially in North America) in dense woods, but probably never forming mycorrhiza.

Development of the carpophores: gymnocarpous in *C. borealis* according to Douglas.

Area: Mostly in northern temperate climates from the boreal zone to the subtropics; probably absent or rather rare in the tropics; one introduced species in South America.

Limits: The separation from *Hygrocybe* does not seem to be very difficult if it is kept in mind that two correlated macroscopical characters (colors and attachment of lamellae) may serve as additional criteria for the separation on the basis of the anatomy of the hymenophoral trama. It is usually possible to tell from the external characters to which genus a specimen belongs.

The group of species around *Hygrophorus hymenocephalus* Sm. & Hesl. which these authors have placed in *Camarophyllus* has a cuticle that is unusual in this genus, and the hyphae of the hymenophoral trama reach larger diameters than the true *Camarophylli*. Its hyphae are devoid of clamp connections. It therefore belongs in the *Tricholomataceae* rather than in the *Hygrophoraceae*.

State of knowledge: The typical and well known species were called sect. *Subturbinata* by Lange (1923) and *Eu Camarophyllus* by Sm. & Hesl. (1942). This group is the only one that is taken into consideration in the enumeration of the species given below. Excepting the doubtful species of this group, there are now 12 species in *Camarophyllus* which may be subdivided into sections later but this re classification will take place only after all the doubtful species have been revised in a monograph. The recent revision of the American species by Smith & Hesler was a great advance in this direction.

Practical importance: None, except for occasional use as edible mushrooms by individual collectors, rarely in the market; only *C. pratensis* is widely known as edible.

SPECIES

Dull colored species: *C. subviolaceus* (Peck) Sing. (Hygrophorus, Peck); *C. Colemanianus* (Blox. ex Fr.) Ricken; *C. subradiatus* (Schum. ex Fr.) Karst.; *C. recurvatus* (Peck) Murr. (Hygrophorus, Peck; Clitocybe praticola Murr., Omphalina australis Murr. are forms or varieties of this species); *C. canescens* (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.)

Pigmentless or nearly pigmentless species: *C. niveus* (Scop. ex Fr.) Karst.; *C. borealis* (Peck) Murr. (if different from *C. niveus*); *C. niveicolor* (Murr.) Sing. (Clitocybe Murr.; Hygrophorus, Sm. & Hesl.); *C. virgineus* (Wulf. in Jacq. ex Fr.) Karst.

Pale cinnamon to yellow or orange species: *C. cremicolor* Murr.; *C. fulvosiformis* Murr.; *C. pratensis* (Pers. ex Fr.) Karst. (Hygropho-

rus, Fr.; Camarophyllus fulvosus (Bolt.) ex Murr.; Hygrophorus ficoides (Bull.) ex Schroeter in Cohn].

KEY TO THE SPECIES

The best key available for North American species is that published in *Lloydia* **5**: 5-6. 1942 by A. H. Smith & Hesler.

3. **NEOHYGROPHORUS** Singer, nom. nov., stat. nov.

Type species: Hygrophorus angelesianus Sm. & Hesl.

Syn.: Hygrophorus subgenus Pseudohygrophorus Sm. & Hesl. *Lloydia*, **5**: 6. 1942.

Characters: those of the preceding genus but spores amyloid; trama reddening with KOH; hymenophoral trama consisting of hyphae often larger than 7 μ in diameter (reaching 12.5 μ in diameter). On the ground.

Development of the carpophores: unknown but probably gymnocarpous.

Area: Western North America (Olympic Mts.).

Limits: This genus is easily distinguishable from all other *Hygrophoraceae* by its amyloid spores. The author has studied the type specimens of the type species in order to be able to point out possible relations with the *Tricholomataceae*, especially the tribus *Lentinelleae* (genus *Cantharellula*, etc.). However, this species, by virtue of its decidedly strongly elongated basidia, its viscid pileus, and the typical *Camarophyllus* lamellae does not appear to have any close affinities with non-hygrophoraceous groups. While there is a striking similarity between this species and similarly colored species of *Camarophyllus*, there is no such similarity between it and *Cantharellula* subgenus *Eucantharellula*. *Neohygrophorus* differs from the subgenus *Eu-Cantharellula* as well as from the other subgenera of *Cantharellula* either because of the lack of incrusting pigment, or because of the characters of its lamellae or the surface of its pileus, or because of the abundance of clamp connections. *Neohygrophorus* is somewhat intermediate between *Camarophyllus* and *Hygrocybe* since its hymenophoral trama is more like that of *Hygrocybe* sect. *Coccineae* whereas its macroscopical characters are closer to *Camarophyllus*.

SPECIES

N. angelesianus (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.)

4. HYGROCYBE (Fr.) Karst.

Hattsvampar (*Bidr. känn. Finl. Nat. Folk* 32 : XVII. 1879 [55]

Type species : *H. miniata* (Fr.) Karst.

Syn : *Agaricus*, trib. *Clitocybe*, subtribus *Hygrocybe* Fr., *Syst. Mycol.* 1 : 101. 1821.

Hygrophorus, trib. *Hygrocybe* Fr., *Epicrisis* p. 329. 1838.

Godfrinia R. Maire, *Rech. cyt. tax. Basidiomyc.*, p. 116. 1902 (Type : *G. conica*).

Characters : those of the family ; pileus viscid or dry, often bright red (near «spectrum red») or bright (lemon) yellow, often the former fading into the latter, or blending into a fire red-orange, more rarely livid violet, green, rose color, vinaceous, etc., or with dull colors (grayish fuscous pigments), or without any pigment ; in the latter case (i. e. if with dull or no pigment) the lamellae are non-decurrent, while in the bright colored forms they are either decurrent, adnexed to subdecurrent, or adnexed to adnate sinuate; spores pure white in print, nonamyloid, never blackening, uninucleate or more rarely binucleate (according to Kuhner); basidia 4 spored, or 2 spored ; cystidia sometimes present, filamentous ; pseudocystidia none ; basidia not blackening in age ; hymenophoral trama subregular-subirregular and then many hyphae broader than 7 μ, or strictly regular ; stipe longitudinally innately striate or glassy smooth, dry or glutinous ; context mild, more rarely bitter ; latex none. In open fields, meadows, mountain slopes, lawns, etc., more rarely in the dense woods and tropical hammocks, rarely on wood, usually on the soil or on sand dunes, in the mud of swamps, etc., probably never mycorrhizal.

Development of the carpophores : incompletely known, probably gymnocarpous at least in the majority of the species ; certainly so in *H. miniata* according to Douglas.

Area : Nearly cosmopolitan, from the sea shore to the alpine region, and from the arctic to the tropics, in all continents excepting the Antarctica ; only introduced species known in Southern South America.

Limits : The genus is usually easy to distinguish macroscopically.

[55] Karsten misspells the name in this paper *Hydrocybe* instead of *Hygrocybe*. This is definitely an error inasmuch as Fries as the original author is cited by Karsten. Unfortunately, Murrill has taken up Karsten's spelling which will cause nomenclatorial trouble if and when the subgenus *Hydrocybe* of *Cortinarius* is given the rank of an autonomous genus.

The absence of a latex and pseudocystidia separates it from *Bertrandia* which is otherwise reminiscent of *Hygrocybe* sect. *Conicae.*

There are several species which were formerly considered as *Camarophyllus* rather than *Hygrocybe*. But they all have the hymenophoral trama as in *Hygrocybe*, according to the key, and the fact that they have either binucleate spores (according to Kühner) or are closely related to species with binucleate spores and typical *Hygrocybe* colors makes the hiatus between *Camarophyllus* and *Hygrocybe* still more distinct.

In contrast to this, several species have been described in *Hygrocybe* that in the author's opinion do not belong in the *Hygrophoraceae* at all (see p. 221).

State of knowledge: Thanks to the efforts of several European authors, and especially to the studies on North American species by A. H. Smith & Hesler, the genus *Hygrocybe* is now comparatively well known. This is, however, one of the genera where complete indications on the characters of the fresh specimens are essential because they look very different when dried in many cases, and do not reveal their bitter taste in herbarium specimens; also, the structure characteristic for viscid or glutinous surfaces on the pileus and the stipe are not always demonstrable on dried material and should be noted carefully immediately after collecting. Because of this, many tropical species which have been available to modern taxonomists only in dried condition, can not yet be inserted in our classification with certainty. Twenty two species are considered as sufficiently known.

Practical importance: Probably all species (excepting perhaps *H. Reai* which, however, hardly remains bitter after cooking) are edible, and can be used in many ways. They make a beautiful dish because of their strong color. They are rarely sold in the markets. *H. conica* has been suspected to be deadly poisonous but the alleged poisoning should be acknowledged with some doubt as many amateurs have eaten this species without any ill effects in all parts of Europe and North America.

SPECIES

Sect. 1. **TRISTES** Bat. (1910). (*Camarophyllus*, sect. *Fornicati* Bat. 1910; sect. *Orini* Bat. 1910; sect. *Emarginatae* Lange 1923). Pigment of the pileus and lamellae not bright colored, either practically absent, or dull colored (gray to fuscous); epicutis of the pileus

not well differentiated, never formed by erect filamentous hyphae which are imbedded in a glutinous mass; stipe not truly viscid; spores sometimes binucleate (in *H. ovina*, according to Kühner); hymenophoral trama subregular.

Type species: H. nitrata (Pers. ex Fr.) Karst.

H. fornicata (Fr.) Sing. (Hygrophorus, Fr.; Camarophyllus, Karst.; Hygrophorus streptopus Fr.; Hygrophorus distans Berk.); *H. nitrata* (Pers. ex Fr.) Karst.; *H. ovina* (Bull. ex Fr.) Kühner [Hygrophorus, Fr.; Camarophyllus, Karst.; Hygrophorus metapodius (Fr.) Fr.].

Sect. 2. COCCINEAE Fayod (1889). (= *Puniceae* Fayod 1889, descr. exclusa; *Pseudocamarophyllus* Sm. & Hesl. 1942; *Miniatae* Sing. 1943; *Inopodes* Sing. 1943). Edge of the lamellae homomorphous; pellicle not provided with a differentiated epicutis consisting of a layer of erect filamentous hyphae imbedded in a gelatinous mass; hymenophoral trama subregular; stipe not distinctly glutinous or viscid, sometimes innately longitudinally fibrillose-striate; spores, as far as known, uninucleate; subhymenium not strongly gelatinized; pigments always bright red or yellow.

Type species: H. coccinea (Schaeff. ex Fr.) Karst.

Subsect. Coccineae (Bat. 1910 ut subsect. *Coccinei* sectionis *Lactorum*). (= *Pseudocamarophyllus* subsect. *Laevi* Sm. & Hesl. 1942). Pileus smooth in wet and dry condition; stipe not longitudinally striate; lamellae adnexed, adnate, or decurrent.

Type species: H. coccinea (Schaeff. ex Fr.) Karst.

H. coccinea (Schaeff. ex Fr.) Karst. (Hygrophorus, Fr.); *H. pulcherrima* Fayod; *H. quieta* (Kühner) Sing. (Hygrophorus marginatus Peck sensu Kühner non Peck; Hygrophorus quietus Kühner); *H. parvula* (Peck) Murr.

Subsect. Squamulosae (Bat. 1910 ut subsect. *Squamulosi* sectionis *Lactorum*) [= sect. *Squamulosi* (Bat.) Konr. & Maubl. 1924 37; sect. *Pseudocamarophyllus* subsect. *Squamulosi* (Bat.) Sm. & Hesl. 1942]. Pileus innately lacerate squamulose, especially in the center when dry (not dried), less so, or smooth, when humid and near the margin; lamellae adnexed to adnate or decurrent; pileus usually dry (not distinctly viscid or glutinous).

Type species. H. turunda (Fr.) Karst.

H. turunda (Fr.) Karst. sensu Karst. (Hygrophorus, Fr.); *H. Cantharellus* (Schw.) Lange (Agaricus. Schw.; Hygrophorus, Fr.; Camarophyllus, Murr.); *H. miniata* (Scop. ex Fr.) Karst. (Hygrophorus, Fr.) with several forms or varieties; *H. sicanctica* Sing.

Subsect. Inopodes (Sing. 1943 ut sectio). (= Sect. *Euhygrocybe* subsect. *Obtusa* Sm. & Hesl. 1942, pp. ?). Pileus dry or viscid and drying out rapidly, not squamulose when drying out; stipe innately longitudinally fibrillose-striate; lamellae never decurrent.

Type species : H. punicea (Fr.) Karst.

H. punicea (Fr.) Karst (Hygrophorus, Fr., an sensu Sm. & Hesl.?, non sensu Fayod); probably also *H. Marchii* (Bres.) Sing. (Hygrophorus, Bres.) and *H. laetissima* (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.).

Sect. 3. CONICAE Fayod (1889) (= *Laeti*, subsect. *Campanulati* Bat. 1910; *Euhygrocybe* Sm. & Hesl. max. e parte, praec. subsect. *Conici* Sm. & Hesl. 1942). Pigments bright red or yellow, pinkish vinaceous, or none; pileus often glutinous; stipe often innately fibrillosely striate, or at least not glutinous in most cases; hymenophoral trama strictly regular, consisting of parallel hyphae (Pl. XXII, 3); epicutis of the pileus not consisting of erect hyphae; spores not binucleate; basidia frequently of the *Godfrinia* type; spores mostly binucleate (Kühner); context sometimes blackening, never reddening, mild to the taste; cheilocystidia usually none but (pleuro-) cystidia often present.

Type species : H. conica (Scop. ex Fr.) Karst.

Subsect. Conicae (Sm. & Hesl. 1943). Pileus conical at least in youth.

Type species : H. conica (Scop. ex Fr.) Karst.

H. conica (Scop. ex Fr.) Karst. (Hygrophorus, Fr.; Godfrinia, R. Maire); *H. nigrescens* (Quél.) Kühner (Hygrophorus, Quél.; Hygrocybe pseudoconica Lange), if specifically different from *H. conica*; – *H. acutoconica* (Clem. in Woods) Sing. [Mycena, Clem. in Woods; Hygrophorus, A. H. Smith; Hygrophorus persistens (Britz.) Britz.; Hygrocybe, Sing.; Hygrocybe constans Lange; H. Langei Kühner; Hygrophorus conicus ssp. Rickenii R. Maire], *H. cuspidata* (Peck) Murr. (Hygrophorus, Peck); *H. foliirubens* Murr. — perhaps also *H. amoena* (Lasch) Ricken (Hygrophorus, Quél.; Hygrophorus calyptraeformis Berk.; Hygrocybe, Fayod), and, according to Kühner: *H. obrussea* (Fr.) Karst. *H. spadicea* (Scop. ex Fr.) Karst. (Hygrophorus, Fr.) is intermediate between section *Tristes* and section *Conicae*.

Subsect. Obtusae (Sm. & Hesl. 1942) Pileus obtuse.

Type species : H. huronensis (Sm. & Hesl.) Singer.

H. huronensis (Sm. & Hesl.) Sing.[44] (Hygrophorus, Sm. & Hesl.);

[44] White forms have been observed among groups of *H. flavescens* which are indistinguishable from *H. huronensis*.

H. flavescens (Kauffm.) Sing. (*Hygrophorus puniceus* var. *flavescens* Kauffm.; *Hygrophorus flavescens* Sm. & Hesl.)

Sect. 4. **SUBGLUTINOSAE** Sing. (1943). Pigments always bright colored; edge of the lamellae homomorphous; subhymenium not gelatinized and broad; spores uninucleate; cystidia and cheilocystidia none; epicutis of the pileus not strongly developed, its hyphae not strictly erect; stipe glutinous or distinctly viscid; hymenophoral trama subregular (not strictly regular, i. e. its elements not parallel with each other as in sect. *Conicae*).

Type species : H. psittacina (Schaeff. ex Fr.) Karst.

H. psittacina (Schaeff. ex Fr.) Karst. (Hygrophorus, Fr.); probably also *H. nitida* (Berk. & Curt.) Murr. (Hygrophorus, B. & C.); *H. flavifolia* (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.); *H. ceracea* (Wulf. apud Jacq. ex Fr.) Karst. (sensu Sm. & Hesl. non Bres.; Hygrophorus Fr.); *H. chlorophana* (Fr.) Karst. (Hygrophorus, Fr.); *H. minutula* (Peck) Murr. (Hygrophorus, Peck); *H. Reai* (R. Maire) Lange (Hygrophorus, Mre.).

Sect. 5. **LAETAE** (Bat. 1910, ut *Hygrophorus*, sect. *Laeti*) em. (= *Puniceae* Fayod 1889, typo excluso; *Glutinosae* Kühner 1926; *Viscidipedes* Sm. & Hesl. p. p. 1942). Pigments not always bright colored; edge of the lamellae often distinctly heteromorphous because of the cheilocystidia (sometimes almost devoid of them); subhymenium gelatinized and broad; spores often binucleate (according to Kühner); epicutis of the pileus strongly developed, consisting of erect filamentous hyphae imbedded in a glutinous layer.

Type species : H. laeta (Pers. ex Fr.) Karst.

Subsect. **Laetinae** (Sm. & Hesl.) Sing. (1943). (= *Viscidipedes*, subsect. *Laeti* Sm. & Hesl. 1942). Carpophores bright colored; cheilocystidia mostly distinct when studied on fresh material.

Type species : H. laeta (Pers. ex Fr.) Karst.

H. laeta (Pers. ex Fr.) Karst. (Hygrophorus, Fr.; Hygrophorus Peckii Atk.; Hygrocybe roseiceps Murr.); probably also *H. hondurensis* Murr. (Hygrophorus, Sm. & Hesl.) and *H. sciophana* (Fr.) Karst. (sensu Konr. & Maubl. non Cooke; Hygrophorus, Fr.).

Subsect. **Obscurinae** (Sm. & Hesl.) Sing. (1943) (= *Viscidipedes* subsect. *Obscuri* Sm. & Hesl. 1942). Carpophores dull colored; cheilocystidia usually not distinct.

H. unguinosa (Fr.) Karst. (Hygrophorus, Fr.).

KEYS TO THE SPECIES

The key published by Smith & Hesler for the North American species can be used for this continent (*Lloydia* **5**, 24-27, 1942) Other keys are those by Lange, especially in his *Flora Agaricina Danica*, treating the species observed in Denmark

5. BERTRANDIA Heim

Rev. Mycologie **1**: 224, 1936

Type species : *B. astatogala* Heim.

Characters : those of the family; pileus conical with involute margin, blackening, lamellae sinuato-free, white, becoming grayish; spores hyaline, then becoming gray and black in spots or reticulate inside the wall; basidia not quite six times as long as the longer diameter of the spores but equally voluminous as compared with the basidia of other *Hygrophoraceae* being rather broad above as well as at the base, blackening, 4 spored; pseudocystidia making the edge of the lamellae heteromorphous; hymenophoral trama regular; stipe fibrous; context with abundant, watery, transparent latex. On the soil.

Development of carpophores : unknown, probably gymnocarpous.

Area : Tropical Africa (Madagascar).

Limits : do not present a problem.

State of knowledge : The only species known has been completely described.

Practical importance : unknown, if any.

SPECIES

B. astatogala Heim.

TRICHOLOMATACEAE Roze

(ut Tricholomées, *Bull Soc Bot Fr* **23**: 51, 1876, nom nud, *ibid* p 112, 1876; Van Overeem, *Bull. Jard Bot. Buitenzorg* **9**: 19, 1927; Heim (ut *Tricholomaceae*, *Treb. Mus Cienc. Nat Barcelona* **15**: 86 1934; Singer, *Ann. Mycol.* **34**: 328, 1936.

Syn.: *Schizophyllaceae* Roze, l c, p 51 and 108 (ut Schizophyllacées); Quel, *Fl. Mycol.* p, 365, 1888.

Mycenaceae Roze, l. c., p. 51 and 109 (ut Mycenées,: Van Overeem in Van Ov & Weese, *Ic Fung Malayens* **14-15**: 4 1926.

Marasmiaceae Roze, *l. c.*, p. 51 and 108 (ut Marasmiées), Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 13. 1927
Clitocybaceae Roze, *l. c.*, p. 51 and 112 (ut Clitocybées); Van Overeem, *l. c.*, p. 21.
Omphaliées Roze, *l. c.*, p. 108
Collybiées Roze, *l. c.*, p. 109.
Pleuropodées Roze, *l. c.*, p. 112
Amarillariées Roze, *l. c.*, p. 113
Agaricacei Schroeter in Cohn, *Krypt. Fl. Schles.*, *Pilze* 3(1), 519. 1888 (non *Agaricei* Fr.).
Pleurotaceae Van Overeem, *l. c.*, p. 20.
Lentinaceae Van Overeem, *l. c.*, p. 12.

Type genus: *Tricholoma* (Fr.) Quél.

Characters: Carpophores not combining all the characters of the *Hygrophoraceae*, i. e. not combining bilateral hymenophoral trama with nonamyloid spores and non-free lamellae; not combining elongate (more than 5.5 times longer than the spores) basidia without carminophilous granulation, with clamped hyphal septa and simple non crowded lamellae; not combining blackening laticifers and basidia and spores with the presence of a watery latex. Pileus and stipe never both covered with a thick epithelium. Stipe never with a cortina that is attached to the margin of a marginate bulb. — Lamellae rarely subfree, usually concurrent, adnexed, adnate, sinuate, or decurrent (if the lamellae are subfree, the spores are uninucleate at the time of discharge); hymenophoral trama intermixed, irregular, subregular, or regular, rarely bilateral (and then spores uninucleate and amyloid), never inverse; spores in spore print pure white, cream color, light creamy pink, very pale drab, light greenish, or pale sordid grayish, never deep or bright colored; wall simple or indistinctly complex, rarely well differentiated into endo-, epi-, and exosporium (and then round in outline, and without any trace of a germ pore), nonamyloid, amyloid, or rarely pseudoamyloid (and then also with pseudoamyloid hairs on the pileus); basidia sometimes of the *Lyophyllum* type (tribus *Lyophylleae*) but more often without carminophilous granulation; sterigmata (1) 2 (3) 4; cystidia or pseudocystidia present or absent; stipe central or eccentric, or lateral, or absent, never with a truly basal volva in mature specimens, rarely with latex (*Mycena* p. p., *Lactocollybia*, p. p.); with amyloid or nonamyloid, partly gelatinized or non gelatinous trama, its hyphae with thin or thick walls, homoiomerous, sometimes with separation zones between the pileus and the stipe, the latter, horny and sometimes string like (chordaceous), with

or without a fibrillose lacerate basis (from the basal tomentum). Taste mild, bitter, or acrid. On the ground in woods and on all kinds of decaying substrata (most frequently), also on living hosts (*Russulaceae*, and *Cormophyta* of various families), among deep moss, on charcoal, on earth, sand, and peat in meadows, fields, on lawns, in gardens, in deserts and steppes, tundras, prairies, marshes, etc.

Limits: The limits of this family have been discussed in the *Hygrophoraceae* (p. 141). They are also in need of clarification regarding the *Crepidotaceae*, *Paxillaceae*, *Cortinariaceae*, *Agaricaceae*, *Amanitaceae* and *Rhodophyllaceae*.

1) *Crepidotaceae*[1]. Some authors have considered the genus *Dochmiopus* Pat. as belonging in the *Tricholomataceae* (or an equivalent group, rather than the *Crepidotaceae* (or an equivalent group). However, *Dochmiopus* cannot be distinguished generically from *Crepidotus* which is the type genus of the *Crepidotaceae*. The color of the spores under the microscope, much deeper than in any genus of the *Tricholomataceae* will prevent from an erroneous misdetermination of the family. The spore print color is not pink as indicated by some authors but rather a pale melleous of the color observed in *Paxillus*, and varying all the way to a rather deep brown, so, consequently, *Crepidotus* and its various sections cannot be compared with the *Tricholomataceae*, and the author does not think that they are related to any of them. The genus *Ripartites*, even more similar to the *Tricholomataceae*, appears to be too close to *Crepidotus* to be removed from the *Crepidotaceae*.

2) *Paxillaceae*. Some authors consider the very pale spored genus *Hygrophoropsis* as belonging in the *Tricholomataceae* rather than in the *Paxillaceae*. Since the author is firmly convinced that *Hygrophoropsis* is closely related to *Paxillus*, it is necessary to elaborate on the diagnosis of the families concerned, adding, here in the *Tricholomataceae*, that forms with repeatedly forked decurrent lamellae, soft context, numerous clamps, small nonamyloid spores, and nonamyloid tissues belong in the *Paxillaceae*, not in the *Tricholomaceae*.

3) *Cortinariaceae*. The genus *Leucocortinarius* which might easily be taken for a genus of the *Tricholomataceae*, and as a matter of fact, has been taken as such by most authors, except Lange, has been

[1]) The genus *Phaeomycena* which is close to the *Crepidotaceae* microscopically, and close to the *Tricholomataceae* macroscopically, is tentatively taken into the latter family. For a more detailed discussion of its characters and position, see there, p. 308.

transferred to the *Cortinariaceae* by the author because of the binucleate spores (according to Kühner), and the obvious similarity of all characters (except the smoothness and paler color of the spores) with the genus *Cortinarius*. It would be next to *Tricholoma*, if left in the *Tricholomataceae*, yet, the subcortinate forms of *Tricholoma* which might be confused with it, differ in having no clamp connections and no marginate bulb, whereas *Leucocortinarius* has both. Albino-forms of *Inocybe* differ from the cortinate species of *Tricholoma* in thicker-walled spores and the presence of clamp connections, from *Tricholomopsis* in terrestrial growth, from both in the presence of metuloids.

4) *Agaricaceae*. The species without appreciable pigment in the spores and with nonpseudoamyloid spore walls that were commonly considered as belonging in *Lepiota* in the broad sense, i. e. the *Agaricaceae* in the modern sense, are difficult to separate from the *Tricholomataceae*, at least as far as a short and precise definition in words is concerned. In spite of the fact that *Cystoderma* has been removed from *Lepiota* by Kauffman, and combined with *Armillaria*, and in spite of the fact that *Smithiomyces* was considered as near *Amanita* by Murrill, it seems to the author that the affinity of these genera is much closer with the *Agaricaceae* than with either *Tricholomataceae* or *Amanitaceae*. The same is true as far as *Drosella* is concerned. Theoretically, all these genera, except *Cystoderma*, can easily be separated from the *Tricholomataceae* by their free lamellae, but actually, the difference between free and subfree is not always very definite, and certainly hard to understand for the beginner. Therefore, it is necessary to state that those genera that have either a distinct epithelium on pileus and stipe, or a heteromerous cuticle are considered as belonging to the *Agaricaceae* rather than to the *Tricholomataceae*, and the same is true for those genera which have a hymeniform epicutis and cream colored spore print. In all these cases, the affinity with the *Agaricaceae* is underscored by the macroscopical appearance that (except for the more adnate lamellae of *Cystoderma*) fits, word by word, the Friesean diagnosis of *Lepiota*. This view, especially as far as *Cystoderma* is concerned, is confirmed by the indication of binucleate spores in *Cystoderma amianthinum* and *C. carcharias* by Kühner.

5) *Amanitaceae*. The problem here is similar to that of the delimitation of *Tricholomataceae* and *Agaricaceae*. The *Amanitaceae* are easily separated from the majority of the *Tricholomataceae* by the bilateral hymenophoral trama. Bilateral trama is, within the *Tricholomataceae*, known only in the tribus *Biannularieae*, and in this tri-

bus the lamellae are not free. In *Armillaria* (more than in *Catathelasma*), the attachment of the lamellae may often be very slight, and in some *Amanitaceae*, the lamellae are not quite free but can at best be called subfree. Also, the spores are amyloid in these *Tricholomataceae* with bilateral trama, and some of the *Amanitaceae* likewise have amyloid spored species included. Among the forms with subfree lamellae, amyloid spores, bilateral hymenophoral trama and simple to double veil — those with uninucleate spores are kept in the *Tricholomataceae*, and those with binucleate spores are kept in the *Amanitaceae*. Those with nonamyloid spores are also considered as *Amanitaceae*. While it is quite obvious that *Amanita*, subgenus *Pseudoamanita* and *Limacella* belong in the *Amanitaceae* because of binucleate spores, it is not quite clear whether *Rhodotus* and *Termitomyces* have binucleate or uninucleate spores. If the spores were not binucleate, the diagnosis of the *Amanitaceae* must be revised, or these genera must be taken into another family, perhaps back into the *Tricholomataceae*. While waiting for further information on the cytology of these genera, one is certainly impressed by the similarities existing between them and other *Amanitaceae* rather than between them and other families; consequently their position among the *Amanitaceae* appears as the only logical one at present.

6) *Rhodophyllaceae*. The genus *Rhodocybe* has generally been thought to be close to *Tricholoma*, the type genus of the family *Tricholomataceae*. However, the spores of some species form all kinds of transition from merely warty to angular, and the absence of clamp connections does not seem to put them close to *Tricholoma* since rough, to angular pink spores are unknown in that genus, while the pink-spored genus *Lepista* is separated by the presence of clamp connections. Under these circumstances, it would not be natural to classify *Rhodocybe* with the *Tricholomataceae*, and far from the genera *Clitopilus* and *Rhodophyllus* that are closely allied to it. It should therefore be summarized: forms with spores that are pink in print and angular in end-view (or in any view) are taken to the *Rhodophyllaceae* rather than the *Tricholomataceae*. This, however, is not the most troublesome problem since it concerns only the position of a genus with well defined characters. However, there are species of *Rhodophyllus* that fail to reveal any type of angular outline in their spores. This might cause their confusion with genera of the *Tricholomataceae*. However, they can be spotted by the following characters which, when combined in a species, should be sufficient to reveal its generic

identity with *Rhodophyllus*: Spore print pink, spore wall nonamyloid, slightly thickened but simple, stramineous in high magnification, pale pinkish-stramineous under low power; clamp connections absent; basidia comparatively voluminous. It will be advantageous in any suspicious case, to check whether the species in question does not show all the essential characters of *Rhodophyllus* except the angular spores which, if present, would have immediately revealed their identity.

The delimitation of the *Tricholomataceae* is also difficult at another level, viz. the separating line between the *Agaricales* and such genera as *Leptotus*, *Campanella*, and *Favolaschia*. As for the discussion of this problem, the reader is referred to these genera on one hand, and to the chapter on phylogenetic theories in the introduction on the other hand.

Phylogeny: The *Tricholomataceae* are the key family for those who attempt to derive the *Agaricales* or part of them from the *Aphyllophorales*. Assuming that this theory were correct, it would be logical to consider the *Tricholomataceae* as the most primitive family among the *Agaricales*. There are, however, also good reasons for deriving the *Tricholomataceae* not directly from any *Aphyllophorales* but rather from the *Hygrophoraceae*, a family which must originally have been much more versiform in many regards. It is, in fact probable that most or all tribes of the *Tricholomataceae* are merely ramifications of a line that eventually goes back to the *Hygrophoraceae* or forms analogous with them but no more in existence, or not yet known. Thus, *Catathelasma* shows many indications that would point to its origin from a hypothetical amyloid spored *Hygrophorus*; *Cantharellula* and related genera would go back to *Neohygrophorus*; *Oudemansiella* would go back to a hypothetical veiled *Hygrocybe*, etc. Fayod already sought the origin of the *Mycenae* (or rather what we call *Marasmiellus*) in the genus *Hygrocybe*, and *Laccaria* might easily be considered as a *Hygrocybe* where the trama of the lamellae is enlarged at the expense of the diameter of the hymenium (i. e. the length of the basidia). *Oudemansiella* has actually been transferred to the *Hygrophoraceae* by Van Overeem (1928). Indeed, very little difficulty is encountered by those who attempt to design a scheme by which all *Tricholomataceae* are considered as descendants of the *Hygrophoraceae*. This scheme should not be forgotten when the relationship between the *Tricholomataceae* and certain *Leptotaceae* is discussed.

KEY TO THE TRIBES

A. Spore walls, tissue, and epicutis all neither amyloid nor pseudoamyloid.

B. Basidia with carminophilous granulation (*Lyophyllum*-basidia)

Lyophylleae, p. 163

B. Basidia without carminophilous granulation both in the basidiole stage as in mature stage

C. Lamellae splitting longitudinally ; stipe absent, or lateral, often a pseudostipe present ; abhymenial hairs more or less differentiated

Schizophylleae, p. 259

C. Lamellae not splitting longitudinally ; consequently abhymenial hairs not differentiated ; stipe present or absent ; pseudostipe present or absent

D. Pleurotoid habit and cylindric spores never occurring at the same time ; pleurotoid and gelatinized (partly or entirely) trama never occurring at the same time ; metuloids rarely present

E. Pileus without strongly differentiated epicutis, i. e. the uppermost layer not different from the trama of the pileus, or dense, or at least its elements not containing true dermatocystidia, dermatopseudocystidia, broom-cells, or diverticulate hyphae, never arranged in a hymeniform or palisadic epicutis ; pseudocystidia none ; latex none ; habit of the carpophores omphaloid, collybioid, pleurotoid, clitocyboid or tricholomatoid, rarely marasmioid

F. Clamp connections present ; black rhizomorphs or a gelatinized cuticle present ; stipe insititious ; habit marasmioid (see *Hemimyceneae* p. 284).

F. Not combining these characters

G. Stipe with diverticulate elements ; cheilocystidia prominent ; habit marasmioid or collybioid.

(see *Hemimyceneae*, p. 284)

G. Not combining these characters (see H_1, H_2, H_3)

H_1. Hymenophore venose ; metuloids pseudoamyloid (see *Lentineae*, p. 260).

H_2. Hymenophore absent or indistinct ; pileus replaced by a physaloid or pezizoid organ that bears the hymenium on its upper or lower side, or indiscriminately (see *Hemimyceneae*, p. 284).

H_3. Carpophores usually with a distinct lamellate hymenophore and distinctly pileate, the pileus usually bearing the hymenium on the lower side *Clitocybeae*, p. 171)

E. Pileus with a strongly differentiated epicutis, or with latex, or with some kind of dermatopseudocystidia ; habit mycenoid, collybioid, marasmioid, omphaloid, rarely pleurotoid-marasmioid, i. e. marasmioid with eccentric or lateral or spurious stipes, very rarely clitocyboid or tricholomatoid ; latex sometimes present.

I. Epithelium present or the central area of the pileus covered with a hymeniform epicutis; hyphae without clamp connections; pigment incrusting the hyphal walls or membranal; habit clitocyboid or tricholomatoid; cystidia none; cheilocystidia sometimes differentiated but not very striking. (see *Clitocybeae*, p. 171)

I. Not combining these characters; habit never clitocyboid or tricholomatoid.

J. Epicutis hymeniform, interspersed with epicuticular hairs, or epicutis forming an epithelium, i. e. made up of a thin layer of sphaerocysts. (see *Marasmieae*, p. 314)

J. Epicutis not so. *Hemimyceneae*, p. 284)

D. Carpophores with pleurotoid habit and cylindric spores (cylindric-subfusoid, fusoid, subellipsoid-oblong, allantoid, etc.); or with pleurotoid habit and partly or entirely gelatinized trama; metuloids often present.

K. Context rarely truly gelatinized; spores cylindric, cylindric subfusoid, fusoid, or subellipsoid oblong, allantoid, etc.; if trama slightly gelatinized it is irregular in the hymenophore. *Lentineae*, p. 260)

K. Context partly or entirely gelatinized; spores globose, reniform, ellipsoid, more rarely cylindric, sometimes ovoid; hymenophoral trama often narrow but distinctly regular or subregular; epicutis never with dichophysate structure. *Resupinateae*, p. 251)

A. Spore wall, tissues, or epicuticular elements either amyloid or pseudoamyloid.

L. Hymenophoral trama of young specimens distinctly bilateral; veil present. *Biannularieae*, p. 374

L. Hymenophoral trama never distinctly bilateral but occasionally very indistinctly so in young specimens and then without a veil.

M. Habit of the carpophores pleurotoid, pezizoid, or polyporoid.

N. Spores smooth, nonamyloid, or pseudoamyloid. (see *Marasmieae*, p. 314)

N. Spores smooth or not smooth, strongly amyloid.

O. Spores smooth, rather short ellipsoid to cylindric; carpophores small and very gregarious, pleurotoid or polyporoid. *Panelleae*, p. 256

O. Spores round and almost smooth (and then pseudocystidia present), or finely warty to echinulate; hymenophore always lamellate. (see *Leucopaxilleae*, p. 234)

M. Habit of carpophores not pleurotoid, pezizoid, polyporoid.

P. Habit of the carpophores collybioid, marasmioid, mycenoid, or omphalioid. *Marasmieae*, p. 314

P. Habit of the carpophores clitocyboid or tricholomatoid. *Leucopaxilleae*, p. 234

Tribus LYOPHYLLEAE Kühner

Bull. mens. Soc. Linn. Lyon 7: 204. 1938.

Type genus: *Lyophyllum* Karst.

Characters: those of the family; basidia of the *Lyophyllum* type, i. e. with carminophilous granulation in the mature basidia (Pl. VIII); spore print white; spores smooth or echinate, nonamyloid; hyphae all nonamyloid, with clamp connections; cuticle usually not well differentiated, often hygrophanous, but sometimes, especially in species with bright colored cuticle, provided with a distinct epicutis consisting of small sphaerocysts; pigment incrusting the hyphal walls, or intracellular. On the soil, on trunks and stumps, and on dead leaves, saprophytically, also on carpophores of *Russulaceae* and perhaps other *Agaricales*, parasitically.

KEY TO THE GENERA

A. Fungi growing saprophytically; chlamydospores none

B. Pigment dull colored (gray, grayish fuscous, umber, etc.), or none, and then the basidia long, and the spores smooth. 6. *Lyophyllum*, p. 163

B. Pigment bright colored (amber yellow, tawny, flesh colored, light cinnamon, lemon, ochraceous pink, lavender to deeper lilac, violet blue, blue, carmine, red, etc.), or none (and then not combining long basidia and smooth spores). 7. *Calocybe*, p. 167

A. Fungi growing parasitically; chlamydospores present. 8. *Asterophora*, p. 170

6. LYOPHYLLUM Karst.

Acta Fl. Faun. Fenn. 2: 3. 1881, em.

Type species: *Lyophyllum leucophaeatum* Karst.

Syn.: *Tephrophana* (Fr., ut sectio) Earle sensu Kühner, non Earle (typo excluso).

Characters: those of the tribus; pileus usually more or less hygrophanous, or with a cartilaginous cortical layer, not sericeous except, sometimes, on the margin, not viscid (or not distinctly so), with frequently somewhat opacous surface, with a dull colored (gray, grayish fuscous, umber, etc.), mostly intracellular pigment, more rarely without any pigment (and then the spores never small as in *Calocybe Georgii*, nor echinulate as in *Calocybe constricta*, and basidia always rather large); epicutis never consisting of small sphaerocysts; hymenophore lamellate; hymenophoral trama regular or almost so; basidia often rather elongate in the larger carpophores; cheilocysti-

dia rather inconspicuous and often absent, other cystidia not present in any species; spores smooth, rarely verrucose spinose and round, otherwise varying, according to the species, from globose to ellipsoid or ovoid, and from ellipsoid oblong to cylindric or fusoid or somewhat compressed and subangular; usually discharged from four sterigmata; chlamydospores never formed on the carpophores; stipe often conglobate, or single; veil none. Habit tricholomatoid, clitocyboid, pleurotoid, collybioid, or omphalioid. On the soil, on dead leaves, on wood, charcoal, always saprophytic.

Development of the carpophores: Probably always gymnocarpous.

Area: More common in boreal regions, possibly restricted to non tropical regions.

Limits: Karsten distinguished the type species from all other species that are now incorporated in *Lyophyllum* by the arbitrary character of separable lamellae which were supposed to prove the affinity with *Paxillus*. Singer later (1936) transferred to this genus a large number of species of Fries's *Collybia*, *Clitocybe*, and *Tricholoma*, on the basis of their macroscopical and microscopical characters. A second emendation was proposed by Kühner, who added a cytological character, the carminophilous granulation of the basidia, now considered as the decisive delimiting character of the genus against genera not belonging to the tribus *Lyophylleae*.

As for the genera belonging to the *Lyophylleae*, the limits are clear enough as far as *Asterophora* is concerned. However, a group of smaller (collybioid) species of the genus were originally separated from the genus *Lyophyllum* by Kühner, under the name of *Tephrophana*. Aside from the fact that the type of *Tephrophana* is not a *Tephrophana* as Kühner understands it but a typical *Marasmius*, the existence of a separate unit for the smaller species of *Lyophyllum* is by no means warranted. Kühner also considered as not belonging to *Lyophyllum* the normally pigment less species with white echinulate spores and with small, smooth, ellipsoid spores. i. e. the groups of *Calocybe constricta* and *C. Georgii*. The existence of an undubitable *Calocybe* with rough spores, discovered in Florida by the author, and the existence of a yellow form of *Calocybe Georgii* described and illustrated by Bresadola, and studied by the author, both show that Kühner's opinion, in this instance, was correct. The author has, consequently, modified the key to the genera of the *Lyophylleae* in a manner that takes into consideration the newly revised position of these white species. On the other hand, Kühner seems to favor the exclusion of *L. connatum*

from this genus since it is, as he says, at the border line of the group. It appears that this species is much closer to the *Difformia* group of *Lyophyllum* than to any group of the genus *Clitocybe*. The diagnosis of the genus has therefore been written in a way as to include this species with less conspicuous carminophilous granulation.

State of knowledge : The genus is in need of revision by a monographer. Some species are well known, enough to establish a well founded classification of the genus. However, certain groups are not completely studied as to the delimitation of their species, a task that is complicated by the fact that, in some of these groups, the synonymy has reached such vast proportions that it seems almost impossible to attribute the right name to the right species. The following account of the 23 species known to belong in this genus, is the best that could be given without more detailed monographic studies.

Practical importance : All known species are edible, some are of great local importance, and are constantly sold in the markets.

SPECIES

Sect. 1. **DIFFORMIA** (Fr.) Kühner (1938). Habit of the carpophores tricholomatoid or clitocyboid, mostly characteristically conglobate, even connate at the bases, thus forming large masses of compound carpophores, pilei and stipes rather thick and fleshy; context unchanging; spores globose or ellipsoid; stipe usually broader than 5 mm.; on the soil.

Type species : L. aggregatum (Schaeff. ex Fr.) Kühner [= *L. decastes* (Fr. ex Fr.) Sing.].

L. connatum (Schum. ex Fr.) Sing. (Clitocybe, Gill.); *L. decastes* (Fr. ex Fr.) Sing. (Clitocybe, Quel.; L. aggregatum (Schaeff. ex Secr.) Kühner; Clitocybe, Gillet; Tricholoma, Cost. & Duf.), with two subspecies ssp. *typicum*, and ssp. *cinerascens* (Bull. ex Konrad) Sing. (Agaricus cinerascens Bull. non Fries sec. Konrad & Maublanc); *L. loricatum* (Fr.) Kühner. — Several American species (*Clitocybe multiceps* Peck, *C. elephantina* Murr., *C. tenebricosa* Murr., *Melanoleuca submulticeps* Murr. and others, are merely forms of *L. decastes*, or very closely related.

Sect. 2. **PLEUROTOIDEA** (Quel. em.) Kühner (1938). Habit pleurotoid-tricholomatoid; context very thick, unchanging; stipe thick, tomentose, velvety, or strigose; spores globose. On wood.

Type species: Pleurotus ulmarius (Bull. ex Fr.) Quél. sensu Kühner).

Lyophyllum ulmarium (Bull. ex Fr.) Kühner (Pleurotus, Quél.).

Sect. 3. **TEPHROPHANA** (Fr.) Sing. (1943). Habit collybioid, mostly gregarious with usually rather thin pileus and stipe (but sometimes thick and fleshy), the latter hollow or becoming so in most species, often subcartilaginous, rarely broader than 5 mm., central, rarely excentric and then not growing on wood, but often growing on or between mosses, on sand, on very decayed wood, on charcoal, or on forest soil, in the latter case sometimes with pseudorrhiza; context not blackening nor bluing; spores globose or ellipsoid.

Type species: L. atratum (Fr.) Sing.

Subsect. **Orbisporina** Sing. (1943). Spores globose, or virtually so.

Type species: L. ambustum (Fr.) Sing

L. ambustum (Fr.) Sing. (Collybia, Quél.); *L. implexum* (Karst.) Sing. (Collybia, Karst.); *L. tesquorum* (Fr. sensu Lange, Kühner) Sing. (Collybia, Gillet, Lange; Tephrophana, Kühner).

Subsect. **Ellipsoideosporina** Sing. (1943). Spores ellipsoid.

Type species: L. atratum (Fr.) Sing.

L. palustre (Peck) Sing. (Mycena, Sacc.; Collybia leucomyosotis Cooke); *L. atratum* (Fr.) Sing. (Collybia, Quél.); *L. rancidum* (Fr.) Sing. (Collybia, Quél.); *L. ozes* (Fr.) Sing.; *L. putidum* (Fr.) Sing. (Tricholoma, Karst.); *L. coracinum* (Fr.) sensu Konrad & Maubl.-Bres.); *L. inolens* (Fr. Sing. (Collybia, Quél.); *L. mephiticum* (Fr.) Sing. (Collybia, Karst.); probably also *L. miserum* (Fr.) Sing., at least as described in *Annales Mycologici* 41: 104, 1943 which form is supposed to be the same as *Collybia misera* sensu Lundell & Nannfeldt.

Sect. 4. **NIGRESCENTIA** (Lange) Sing. (1943). Habit tricholomatoid or collybioid; spores globose, ellipsoid cylindric, ellipsoid oblong, fusoid cylindric, etc., often angular in end view, tetraedric, cruciform, or otherwise irregular; context or lamellae, or both, blackening or bluing on bruising or drying; usually on earth or leafmold, solitary or gregarious.

Type species: L. leucophaeatum (Karst.) Karst.

Subsect. **Goniosporina** Sing. (1943). Spores with flattened sides therefore more or less angular in end view, i. e. with the longitudinal axis of the spore pointing toward the objective, or tetraedric, twice tetraedic, rhomboid, sometimes tending to appear cruciform.

Type species: L. infumatum (Bres.) Kühner.

L. infumatum (Bres.) Kühner (Clitocybe ectypa var. infumata Bres.); *L. transforme* (Britz.) Sing. [Tricholoma (Britz.) Sacc.; Clitocybe semi

talis var. trigonospora Bres.; Tricholoma trigonosporum (Bres.) Ricken].

Subsect. **Globisporina** Sing. (1943). Spores globose or nearly so.

Type species : L. immundum (Berk.) Kühner.

L. immundum (Berk.) Kühner (*Tricholoma*, Quél.); also, probably several European species of doubtful standing, and incompletely known characters.

Subsect. **Elongatisporina** Sing. (1943). Spores elongate, fusoid-ellipsoid, fusoid cylindric, ellipsoid cylindric, etc.

Type species : L. leucophaeatum (Karst.) Karst.

L. leucophaeatum (Karst.) Karst. [Collybia Karst.; Tricholoma, Karst.; Clytocibe gangraenosa (vix Fr.) Metrod non al.]; *L. capniocephalum* (Bull. ex Fr. sensu Bres.) Kühner (Collybia, Bres.; Hebeloma, Sacc.); *L. macrosporum* Sing. [Clitocybe ectypa (Fr.) Quél. sensu Bresadola non al.]; *L. semitale* (Fr.) Kühner (Collybia, Quél.).

KEY TO THE SPECIES

Keys to most of the species here enumerated, and, in addition, some doubtful species, have been published in *Annales Mycologici* 41 : 98-105. These keys are partly tentative in delimitation and nomenclature but they are the most complete keys published.

7. CALOCYBE Kühner

Bull. mens. Soc. Linn. Lyon **7** : 211. 1938.

Type species : Calocybe Georgii (Clusius ex Fr.) Kühner [same as *C. gambosa* (Fr.) Sing.].

Characters : Those of the family; pileus always bright colored (never gray, grayish fuscous, umber, etc.), or pigment-less, pigment sometimes incrusting; spores usually small (up to 7 µ long), more rarely longer but then usually echinulate; epicutis often cellular; veil present or more often absent. On soil, on leafmold, on dead wood, in plantations, jungles, on lawns and meadows.

Development of the carpophores : Gymnocarpous, at least in the type species according to Kühner.

Area : In the temperate as well as in the tropical zone, especially in America.

Limits : See under *Lyophyllum*, and *Tricholoma*.

State of knowledge : The genus has been studied rather completely

but it may be expected that there are more tropical species than are described at present. Since there are parallel forms, with and without sphaerocysts forming an epicutis, it would be interesting to study the constancy of this character. At least 13 species are referable to this genus.

Practical importance : Some species are edible, especially the delicious spring species often sold in European markets, *Calocybe gambosa.*

SPECIES

Sect. 1. **GUTTATAE** (Fr.) Sing. *Agaricus,* trib. *Tricholoma,* sect. *Guttati* Fr. 1836; *Tricholoma,* sect. *Albella* Konr. & Maubl., 1924-37). Pigment very little, exceptionally yellow, and then not coloring the whole carpophore uniformly; spores smooth, small; basidia small; habitat outside the woods in temperate regions, often vernal; epicutis not cellular.

C. gambosa (Fr.) Sing. [Tricholoma, Gill.; Lyophyllum, Sing. 1943; Tricholoma Georgii (Clus. ex Fr.) Quél.; Calocybe, Kühner; Tricholoma albellum (Fr.) Quél.]. This species is divided in several forms, or varieties which are considered as related species by some authors.

Sect. 2. **ECHINOSPORAE** (Lange) Sing. (1943, ut sectio gen. *Lyophylli*). Pileus without or with very little pigment; spores and basidia comparatively large; spores echinulate or rough; cellular epicutis none; stipe with (or without) an annular veil; mostly outside the woods.

C. constricta (Fr.) Kühner (Armillaria, Gillet; Tricholoma, Ricken); probably also *Tricholoma leucocephalum* (Fr. sensu) Lange.

Sect. 3. **HETEROSPORAE** Sing. Pileus with incrusting pigment; spores and basidia medium sized (spores about 6-7 µ long; basidia 28-39 × 7.5-9.5 µ), the latter comparatively large, the former echinulate or rough; cellular epicutis none; stipe evelate; in tropical forest.

C. heterospora Sing.

Sect. 4. **PSEUDOFLAMMULAE** Sing. (1943). Pigment of the pileus amber yellow, or wax yellow, perhaps also olivaceous in certain forms, often with more ocher brown or deep red shades; spores smooth; in the woods (mostly coniferous, rarely tropical), more rarely in the subalpine or alpine zone of the mountains, or in swamps.

Type species : C. cerina (Pers. ex Fr.) Kühner sensu Sing. non Kühner.

Species without cellular epicutis: *C. cerina* (Pers. ex Fr.) Kühner sensu Kühner (Tricholoma, Quel. p.p.?; Agaricus Pers. ex Fr. p.p.?); *C. rubra* Rick ex Sing.; perhaps also *C. olivascens* (R. Maire) Sing.; *Tricholoma thujinum* Peck, and *Tricholoma pseudoflammula* Lange.

Species with cellular epicutis: *C. cerina* (Pers. ex Fr., Kühner sensu Sing. (Tricholoma, Quel. p.p.?; Agaricus Pers. ex Fr. p.p.?); *C. Naucoria* (Murr.) Sing. (Agaricus fallax Peck non Lasch); *C. alpestris* (Britz.) Sing.; *C. onychina* (Fr.) Kühner (Tricholoma, Gillet); perhaps also *Tricholoma subcerinum* A. H. Smith.

Sect. 5. **CARNEOVIOLACEAE** Sing. (1943). Pigment of the pileus pinkish buff to lilac pink, or deep violet to rich blue; spores smooth; in the woods and on the open fields, pastures, roadsides, etc.

Type species: *C. ionides* (Bull. ex Fr.) Kühner.

Species without cellular epicutis: *C. carnea* (Bull. ex Fr.) Kühner (Tricholoma, Quel.); *C. persicolor* (Fr.) Sing. (Tricholoma, Karst.); *C. ionides* (Bull. ex Fr.) Kühner (Tricholoma, Quel.; Agaricus fallax Lasch sec. Konr. & Maubl.); *C. cyanella* Sing.

Species with cellular epicutis: *C. cyanea* Sing. and *C. spec.* (Brazil).

KEY TO THE SPECIES

A. Pileus white
- B. Spores smooth; veil none. Europe. — *C. gambosa*
- B. Spores not smooth; veil annuliform. Temperate zone. — *C. constricta*

A. Pileus colored
- C. Spores not smooth, Florida. — *C. heterospora*
- C. Spores smooth.
  - D. Pileus pinkish buff; stipes connate at the bases; epicutis never cellular; growing in open fields, meadows, also along forest roads. European species. — *C. persicolor*
  - D. Not combining these characters
    - E. Pileus not deeply colored, more or less pink, neither yellow nor red, nor brown, olive, violet, blue; lamellae white; epicutis not cellular; on meadows, lawns, in open fields, pastures, etc. European species. — *C. carnea*
    - E. Pileus deeper colored, or at least not pink.
      - F. Pileus with a cellular epicutis.
        - G. Pileus from yellow to yellowish brown, not red or brown-red, lamellae and stipe almost concolorous. — *C. alpestris*, *C. Naucoria*, and *C. cerina* sensu Sing.
        - G. Pileus not so colored.
          - H. Pileus blue or nearly so. Brazil. — *C. cyanea*
          - H. Pileus red (purplish chestnut) or nearly so. Temperate zone, circumpolar. — *C. onychina*

F. Pileus without a cellular epicutis.
I. Pileus not deep violet or blue.
J_1. In temperate woods, mostly under conifers; pileus yellow or brownish yellow. Temperate zone. *C. cerina* sensu Kühner
J_2. In tropical forest, not under conifers; pileus red or nearly so. Brazil *C. rubra*
J_3. In open fields, meadows, etc., especially in spring. Europe. *C. gambosa* var.
I. Pileus deep violet or blue.
K. Pileus a rich blue; spores $4.5 \times 2.5-3$ μ. Tropical Florida. *C. cyanella*
K. Pileus deep violet; spores somewhat smaller. Europe and North America, south to North Florida *C. ionides*

8. ASTEROPHORA Ditmar ex S. F. Gray

Nat. Arr. Brit. Pl. 1: 253. 1821.

Type species: *Asterophora lycoperdoides* (Bull.) Ditmar ex Gray.

Syn.: Nyctalis Fr., *Stirpes Agri Fems.* 3: 58. 1825.

Characters: Those of the tribus; pileus never bright colored; lamellae often somewhat reduced (rather thick and obtuse, narrow and distant), and production of basidiospores reduced (the more so the more abundant the chlamydospores are); chlamydospores always formed, usually on the mycelium, always on and in the carpophores, in the uppermost layer of the pileus from the surface downwards, or in the lower part of the pileus and in the hymenophore; they are brown, stellate (Pl. X) or smooth; habitat: parasitically on *Russulaceae*. Monomethylparamidophenol strongly positive with the context.

Development of the carpophores: Unknown in *A. parasitica*, gymnocarpous in *A. lycoperdoides* (Reijnders).

Area: Not fully established; found in Europe, North America, Cuba.

Limits: The habitat and the manner of reproduction distinguish this genus sufficiently.

State of knowledge: Many dubious species were described in *Nyctalis* but it is probable that the genus *Asterophora* contains only two species. These are completely known.

Practical importance: None. Eichelbaum described a *Nyctalis*

Coffearum causing « splitting disease » of *Coffea* but this species is probably not an *Asterophora*.

SPECIES

A. lycoperdoides (Bull.) Ditmar ex S. F. Gray (Nyctalis asterophora Fr.); *A. parasitica* (Bull. ex Fr.) Sing. [Nyctalis parasitica (Bull. ex Fr.) Fr.].

Tribus CLITOCYBEAE Fayod

(ut Clitocybés), *Ann. Sc. Nat.* VII. **9** : 344. 1889. em.; *Lotsy*, *Vortr. Bot. Stamm.-gesch.* **1** : 711. 1907.

Type genus : *Clitocybe* (Fr.) Quél.

Syn. : Tricholomateae Fayod (ut Tricholomés), *l. c.*, p. 346; *Lotsy*, *Vortr. Bot. Stamm.-gesch.* **1** : 713. 1907 (*Tricholomeae*; Imai, *Journ. Fac. Agr. Hokk. Imp. Univ.* **43** : 64. 1938.
Collybieae Konr. & Maubl. *l. c.* (ut Collybiées); Imai, *l. c.*, p. 113
Armillarieae Imai, *l. c.*, p. 46.

Characters : Basidia not of the *Lyophyllum* type; spores and tissue and epicuticular elements (if present) nonamyloid; lamellae not splitting longitudinally; hymenophoral trama never distinctly bilateral (slightly diverging in outermost layer at times); epicutis not strongly differentiated, except in a few species of *Armillariella* and *Tricholoma* which have clampless septa between the hyphae; pseudocystidia, metuloids and conspicuous cystidia absent; habit clitocyboid, or tricholomatoid, more rarely pleurotoid (and then spores never cylindric, or elongated more than twice their breadth and the trama not gelatinized), or omphaloid (then without cystidia), or collybioid to marasmioid (then without any spherocysts on the cuticle); rhizomorphs either white or black (in the latter case—clamp connections absent between hyphae, and trama not gelatinized, and habit not marasmioid); hymenophore always well developed in mature specimens; carpophores pileate. On various kinds of substrata, parasitical and saprophytical, or symbiotic.

KEY TO THE GENERA

A. Clamp connections present, i. e. most or many septa between hyphae are provided with clamps except in occasional parthenogenetic forms.

Clitocybinae (p. 174)

B. Cheilocystidia large and conspicuous making the edge of the lamellae

distinctly heteromorphous; spores usually short (globose to short-ellipsoid or ovoid) and small to medium, often with slightly thickened walls; base of the stipe attached to white rhizomorphs that lead to decaying wood, or directly attached to decaying wood; pileus fleshy, neither membranous nor tough and reviving, fibrillose, squamulose, squarrose, non-hygrophanous, pileus centrally stipitate. 15 *Tricholomopsis* (p. 194)

B. Cheilocystidia neither large nor conspicuous, or else fungi not combining the characters enumerated above.

C. Spores large and globose, not pure white in print; veil present; carpophores luminescent, pleurotoid, growing on wood

10. *Lampteromyces* (p. 178)

C. Not combining all these characters.

D. Carpophores bright colored, luminescent; spores subglobose and small or medium in size, smooth, the mature walls often slightly thickened, pure white in print, lamellae deeply decurrent; cystidioles present (though not conspicuous), or pseudoparaphyses with all transitions from basidioles to cheilocystidia present.

12. *Omphalotus* (p. 180)

D. Not combining these characters.

E. Fungi developing large, fleshy carpophores on the trunk and the branches of standing trees, more rarely on logs; pigment none or little; spores rather small, rather globose, white in print, with somewhat thickened mature walls; lamellae never decurrent; cystidia and pseudoparaphyses none; stipe central or eccentric, solid; hymenophoral trama regular. 11. *Hypsizygus* (p. 178)

E. Not combining these characters.

F. Habit of the carpophores pleurotoid, or else lamellae decurrent and consistency tough and reviving; hymenophoral trama irregular; lignicolous or on living mosses.

G. Lamellae subclose to crowded, or extremely narrow and forking.

H. Pigment none or virtually absent, at least under the microscope; temperate and boreal.

17. *Pleurocybella* (p. 202)

H. Pigmented species; stipe arising from a pedestal; tropical. (If not arising from pedestal see «J»). 20. *Trogia* (p. 207)

G. Lamellae moderately close to distant, never extremely narrow and forking.

I. Carpophores reviving after having been dried out on the habitat, as soon as moistened; mainly tropical and subtropical.

J. Hyphae and basidia hyaline.

18. *Nothopanus* (p. 203)

J. Hyphae and/or basidia greenish in KOH.

19. *Anthracophyllum* (p. 205)

I. Carpophores not reviving; temperate or boreal (if not temperate or boreal compare « J »).
(see *Omphalina*)

F. Habit of the carpophores not pleurotoid; if consistency is tough or reviving the lamellae are not decurrent.

K. The whole hymenophoral trama very irregular to intermixed; pileus hygrophanous; pigment more or less distinctly incrusting the walls of the hyphae; habit of the carpophores omphalioid; consistency soft-fleshy, but context thin; lamellae distant.
(see *Omphalina*)

K. Not combining these characters.

L. Hymenophoral trama forming a thick layer of regular structure; spores either globose and echinate, or more or less cylindric and voluminous and smooth; cheilocystidia present; lamellae rather thick and somewhat distant; carpophores, especially lamellae, often with blue, lilac, violet, pinkish-vinaceous, rose color, yellow tinge; veil none. 9. *Laccaria* (p. 174)

L. Not combining these characters.

M. Lamellae adnate to deeply decurrent; stipe not cartilaginous (habit clitocyboid); spores smooth, or white in print; veil none 13. *Clitocybe* (p. 182)

M. Not combining these characters.

N. Spores rough and pale sordid pink in print. 14. *Lepista* (p. 190)

N. Not so.

O. Context decidedly fleshy, soft; lamellae always strongly emarginate-sinuate; stipe neither cartilaginous, nor tough, nor thin and tubulose; spore print pure white, rarely very pale cream.

(see *Tricholoma*, p. 218, cf. *Coolia*, p. 233)

O. Context not so; stipe thin and tubulose, and the cortical layer of the stipe more or less cartilaginous or tough; lamellae subfree to adnate, sometimes somewhat sinuate; spore print often pinkish. 16. *Collybia* (p. 197)

A. Septa between hyphae not clamped *Tricholomatinae* (p. 209)

P. Lamellae decurrent or adnato-decurrent.

Q. Spores white in print, wall thin; stipe up to 4 mm broad; veil and black rhizomorphs none; habit omphalioid. 21. *Omphalina* (p. 209)

Q. Spores frequently colored (mostly yellowish) in print, wall some-

times rather thick when quite mature; stipe more than 4 mm broad; veil and black rhizomorphs sometimes present; habit clitocyboid.
22. *Armillariella* (p. 214)

P. Lamellae not decurrent.

R. Carpophores with tricholomatoid habit; spore print not pink, and no pigment bodies occurring inside the spores of herbarium material; lamellae strongly emarginate-sinuate, rarely adnexed; mostly on soil
23. *Tricholoma* (p. 218)

R. Carpophores with mycenoid, collybioid, or pleurotoid habit; mostly on wood

S. Cuticle of pileus not or little pigmented; stipe central; spores sometimes pink in print, but without pigment bodies.
24. *Podabrella* (p. 229)

S. Cuticle of pileus distinctly pigmented; stipe eccentric and somewhat oblique, or spores with pigment bodies, white in print

T. Stipe eccentric and oblique; spores without pigment bodies.
25. *Pleurocollybia* (p. 230)

T. Stipe central and straight or slightly curved, spores of herbarium specimens with strongly colored, solid pigment bodies inside the wall, but fresh spore print white
26. *Callistosporium* (p. 231)

Subtribus CLITOCYBINAE Sing.

Type genus: *Clitocybe* (Fr.) Quél.

Characters: Those of the tribus; clamp connections present except in occasional parthenogenetic forms.

9. LACCARIA Berk. & Br.

Ann. Mag. Nat. Hist. **5**: 370. 1883.

Type species: *Laccaria laccata* (Scop. ex Fr.) Berk. & Br.

Syn.: *Russuliopsis* Schröter in Cohn, *Krypt. F. Schles.*, *Pilze*, p. 622. 1889.

Characters: Pileus dry to subhygrophanous, glabrous to squamulose, smooth to transparently striate when moist; cuticle not strongly differentiated; lamellae rather thick and somewhat distant, moderately broad to extremely broad, usually bright colored (blue, lilac, violet, pinkish vinaceous, rose color, yellow); hymenophoral trama strictly regular to almost regular; spores either oblong and voluminous (11-22 μ long), and then smooth, or short-ellipsoid to globose and then echinate, the spines sometimes curved and arranged in spirals,

nonamyloid; spore print white or « pale Verbena violet »; basidia frequently two spored, otherwise four-spored, without carminophilous granulation, cystidia none, but cheilocystidia mostly present; trama fibrous fleshy, not reviving, nonamyloid; pigments not conspicuous microscopically, not incrusting the hyphal walls, all hyphae with clamp connections. On soil, among deep moss, in clearings, in deep woods, in alpine pastures, along brook beds, on decayed wood, on leafmold, among dead needles, on sandy and on rocky places. Ferric sulphate causing a distinct deep gray discoloration in the species tested.

Development of the carpophores: Seems to be hemiangiocarpous in *Laccaria laccata* (see Reijnders, pl. V, fig. 7).

Area: Cosmopolitan.

Limits: The original diagnosis and the characters enumerated above do not cover all the eventualities that might be expected when certain little known species are studied more carefully. Lange has indicated that the species he calls *Clitocybe sandicina* has all characters except the spores of a *Laccaria*. However, it appears probable that the trama and the pigments are those of *Omphalina* rather than *Laccaria*, and, therefore, no premature emendation of the diagnosis of *Laccaria* has been proposed.

Velenovsky has described a species which he considered as new, *Russuliopsis lineata* Velen., and the author has also found a species in the Altay Mts. which has a dull yellowish gray color but spinose spores. In the latter case, the trama was regular or subregular. This would exclude *Omphalina*. However, the basidia were not studied with aceto-carmine, and it is possible that the specimen belongs to *Lyophyllum*. In *R. lineata* which the author has recollected near Praha, Czechoslovakia, the same possibility exists. Consequently, an emendation of the diagnosis of *Laccaria* in this direction, i. e. including species with dull colored lamellae is unnecessary at present.

Collybia clusilis and *C. vulgaris* turn slowly deep gray with ferric-sulphate, and, if the diagnosis of *Laccaria* would include dull colored species, it may become difficult to separate the genus *Collybia* on this level. However, the gray $FeSO_4$ reaction may be more common among the *Clitocybinae* than we know now, and the spores are so different from those known in *Laccaria* that it would be impossible to maintain *Laccaria* as a genus if the *Collybia clusilis* group should actually become a problem. The author is convinced that this will not be the case in spite of the fact that Fries put *Clitocybe pachyphylla*, which

Lange thinks is the same as *Collybia clusilis*) in the same section as *Laccaria laccata*.

Including only those species that are completely known, the delimitation of the genus *Laccaria* is rather easy. Among the *Clitocybinae*, it is easily distinguishable on the basis of its spore characters, the structure of the hymenophoral trama and the edges of the lamellae, the colors of the lamellae, the thickness of the lamellae, the absence of a veil, and the non pleurotoid habit. The chemical and the ontogenetic characters are not known to be generic.

Considering the limits of the genus, and its most striking characters, one is led to believe that *Laccaria* is most closely related not to *Clitocybe*, or *Omphalina*, or *Collybia*, but to the Japanese genus *Lampteromyces*.

State of knowledge: All the ten species that are admitted in *Laccaria* in the present sense, are well known.

Practical importance *L. laccata*; *L. amethystina*, and *L. trullisata* are known to be edible. Since the first and last of these species often grow in places where other edible mushrooms are rarely found, they may have some local importance in spite of their second grade quality.

SPECIES

Stirps **Trullisata** (with smooth spores): *L. Gruberi* (A. H. Smith) Sing. (Clitocybe, A. H. Smith); *L. trullisata* (Ellis) Peck [Clitocybe, (Ellis) Sacc.].

Stirps **Amethystina** (with echinate pale violet spores): *L. amethystina* (Bolt. ex Fr.) Berk. & Br.; *L. ochropurpurea* (Berk.) Peck.

Stirps **Laccata** (with echinate pure white spores): *L. laccata* (Scop. ex Fr.) Berk. & Br. (Clitocybe, Quél.), with its varieties var. *proxima* (Boud.) R. Maire, var. *roseola* (Batsch ex Fr.) Sing. (= var. bicolor R. Maire); *L. tetraspora* Sing.; *L. ohiensis* (Mont.) Sing. [Clitocybe Sacc.; Laccaria striatula (Peck) Peck]; *L. altaica* Sing. [= Laccaria striatula (Peck) Peck sensu Sing. 1943, non Peck]; *L. echinospora* (Speg.) Sing. [Clitocybe, Sacc.; L. pumila Fayod; L. tortilis (Bolt. ex Fr.) Pat. sensu auct. nonn. (non Bolt. ex Fr.)].

KEY TO THE SPECIES

A. Spores smooth, strongly elongate.
  B. Lamellae yellow. Species occurring in the Rocky Mts. of North America. *L. Gruberi*
  B. Lamellae lilac-pinkish, or dull vinaceous. Species occurring in the Central and Atlantic states of North America, in sand dunes. *L. trullisata*
A. Spores echinate, not strongly elongate, mostly subglobose or globose.
  C. Lamellae deep bluish lilac, e. g. Pl. 45, E 1 (M. & P.) or bluer; spore print « pale Verbena violet ». (R.) or Pl 41, B 2 (M. & P.); sterigmata 2, or 4, or variable in number.
    D. Pileus 10-50 mm broad. *L. amethystina*
    D. Pileus larger. *L. ochropurpurea*
  C. Lamellae pinkish, purplish pink, flesh color, etc. (see table I)

TABLE I

Size of carpophores	Characters of spores	Formae tetrasporae	Formae bisporae
Large to medium, rarely small	ellipsoid, or else globose but not over 10μ; spines smaller than 1μ	*Laccaria laccata*	—
Small to medium	globose, larger than 10μ, but smaller than 12.8μ; spines larger than 1μ	*Laccaria tetraspora*	*Laccaria ohiensis*
Small to medium	globose, larger than 12μ but smaller than 13.5μ; spines smaller than 1μ	(Only unmixed 2- and 4-spored forms of *L. altaica*)	*Laccaria altaica*
Small to very small	globose, 12-23μ in diameter; spines larger than 1μ	—	*Laccaria echinospora* = *Laccaria pumila*

This table shows that, the larger the carpophores, the smaller the spores and vice versa. It also shows that the smaller the carpophores, the more inclination to form bisporous forms. More detailed studies of the spore number and the cytology and sexuality of all these species are needed in order to prove what the author thinks has taken place here: the number of sterigmata has become a specific, fixed character in at least some of the species.

10 LAMPTEROMYCES Sing.

Mycologia 39 : 79. 1947.

Type species : Lampteromyces japonicus (Kawamura) Sing.

Characters : Carpophores distinctly pigmented, rather bright colored on the pileus, pleurotoid, luminescent (Pl. I); pileus not viscid, not hygrophanous, fibrillose; lamellae deeply decurrent; basidia without carminophilous granulation; spore print whitish drab; spores hyaline, smooth, nonamyloid, often thick walled, globose, very large; cystidia indistinct or none; hymenophoral trama regular, consisting of somewhat flexuous or straight, not strongly interwoven hyphae; subhymenium narrow; stipe eccentric or lateral, firm tough, annulate from a persistent veil that consists of filamentous hyphae; context consisting of nonamyloid hyphae with clamp connections. On wood.

Development of the carpophores : Unknown.

Area : Japan.

Limits : This genus is clearly delimited from all other genera of the *Clitocybeae* and *Lentineae*, as well as from all other fungi known.

State of knowledge : The only species that belongs here is completely known.

Practical importance : This is an important poisonous species which has caused serious poisonings in Japan.

SPECIES

L. japonicus (Kawamura) Sing. (Pleurotus, Kawamura; Armillaria, Imai).

11. HYPSIZYGUS Sing.

Mycologia 39 : 77. 1947.

Type species : H. tessulatus (Bull. ex Fr.) Sing.

Characters . Pigment almost none; carpophores nearly tricholomatoid to nearly clitocyboid, but at the same time somewhat pleurotoid because of the frequent eccentricity of the stipe, non luminescent; pileus non hygrophanous and not viscid, often areolate-rimose; cuticle little differentiated; lamellae adnexed or adnate, sometimes decurrent with a tooth, not sinuate, or sinuate-emarginate on one side of

the carpophore; basidia normal in all regards; without carminophilous contents; cystidia absent; spore print pure white; spores globose or subglobose-ellipsoid, nonamyloid, smooth, the wall eventually slightly thickened, diameter smaller than 10 μ mostly around 5 μ; hymenophoral trama regular much like that of typical Clitocybes; subhymenium very narrow, ramose; stipe thick and fleshy, often somewhat eccentric or curved; veil none; context fibrous-fleshy, thick; trama nonamyloid; hyphae with clamp connections. On trunks and branches of living and dead frondose trees.

Development of the carpophores: Unknown.

Area: Circumpolar but more common in America and Eastern Asia.

Limits: Traditionally, this is a « *Pleurotus* ». It differs, however, from that genus in the more or less globose, not quite thin-walled, white spores, in the manner in which the lamellae are attached to the stipe, and in the structure of the trama. The author has formerly attempted to avoid the erection of a new monotypic genus by uniting this species with *Clitocybe*. But the Clitocybes, sect. *Candicantes*, have different habit, and the spores are more or less ellipsoid whith thinner walls; these white Clitocybes are also much different in their habitat requirements, for even if the substratum is wood, the fructifications are never found high up on living trees, and the wood is in a more advanced state of decay.

Hypsizygus is comparable with *Pleurocybella*, at least the stipitate forms. *Pleurocybella* differs, however, in habitat, more eccentric habit, narrower and more decurrent lamellae, much more irregular hymenophoral trama and more fragile consistency.

The clamp-bearing Tricholomas differ in being terrestrial and having clearly sinuate lamellae, strictly central stipe and usually more elongate spores with thinner walls.

State of knowledge: Only three completely known species can be named at present, but only one of them has been located among the species indicated in the older literature.

Practical importance: It is doubtful whether *Hypsizygus tessulatus* causes wood rot on previously undiseased elms. It is, however, certain that this fungus at least contributes to the death of older trees. The carpophores are eaten by the American Indians as well as by a small part of the white population in North America, and by some mushroom hunters in East Asia.

SPECIES

H. tessulatus (Bull. ex Fr.) Sing. (Pleurotus Gillet; Pleurotus « ulmarius » auct. Amer., non sensu Kühner); *H. circinatus* (Fr. ??) Sing. (Clitocybe, Karst. sensu Sing. 1943); also a closely related species collected by A. H. Smith in Oregon (inedit.), and perhaps *Pleurotus craspedius* (Fr.) Gill. sensu Romagnesi.

12. OMPHALOTUS Fayod

Ann. So. Nat. Bot. VII. 9 : 338. 1889

Type species : Pleurotus olearius (D. C. ex Fr.) Gillet.

Syn. : Monadelphus Earle, *Bull. N. Y. Bot. Gard.* 5 : 432. 1909.

Characters : Carpophores intermediate between pleurotoid and clitocyboid in habit ; pileus fleshy, non hygrophanous ; hymenophore lamellate, luminescent when fresh, bright colored as the whole carpophore ; not developing cyanic acid ; spore print pure white ; old spores with slightly thickened walls, subglobose, hyaline ; lamellae deeply decurrent ; basidia normal but some one spored, and some transitions between these (sterigma not discharging a spore : pseudoparaphysoid) and the cystidioles that are often numerous near the edge of the lamellae, can be observed in certain specimens ; the single sterigma of the pseudoparaphyses may even attain enormous size and finally separate from the pseudoparaphysis and float around in the preparations (binucleate conidium ?) ; spores, basidia and hyphae nonamyloid ; hyphae with clamp connections, epicutis little differentiated ; hymenophoral trama irregular to subregular with recognizable axillar trend (near the thin subhymenial layer) ; stipe fibrous, fleshy, central or eccentric ; odor of *Collybia dryophila* ; on decaying wood (stumps and trunks) of both coniferous and frondose trees, usually fruiting in large number ; binucleate mycelium in culture non luminescent, producing oidia (observed by Hanna and the author).

Development of the carpophores : Unknown.

Area : Probably almost cosmopolitan but not represented in boreal and alpine floras.

Limits : This genus has been combined with *Pholiota* subgenus *Flammula*, with *Clitocybe*, and with *Pleurotus*. While its insertion in

Flammula was obviously a mistake, the combination with *Clitocybe* and *Pleurotus* was proposed with the intention of emending the diagnoses of these genera in order to include *Omphalotus*. However *Omphalotus* has so many features characteristic only to its single species, it appears impossible to incorporate it in *Clitocybe* where it would be so isolated that a new subgenus would have to be established for it. Neither from an anatomical morphological, nor from an ecological-chemical point of view, can, in the author's opinion, identity with the genus *Clitocybe* in the classical sense or in the emended sense be claimed. The author has (1943) tentatively put *Omphalotus* in *Armillariella*, however, under the condition that the hyphae of the carpophore are clampless. Recent studies, however, have shown that clamp connections are constantly present. Its identification with *Pleurotus* cannot be admitted under present circumstances considering the much narrower sense in which *Pleurotus* is now conceived. The species left in *Pleurotus* are absolutely not allied to *Omphalotus* from whatever point of view they are examined, unless the substratum is made the decisive factor. The spores are subglobose in *Omphalotus*, and cylindric in *Pleurotus*. The hymenophoral trama is much more irregular (to almost intermixed) in *Pleurotus* than in *Omphalotus*. The subhymenium is much more distinct from the trama and forms a broader layer in *Pleurotus* than in *Omphalotus*; the spore print is not pure white in most species of *Pleurotus*, and the stipes are, in an average, more eccentric in *Pleurotus*.

State of knowledge : The author admits, at present, only one single species which may be divided into several races (geographical or ecological); others may prefer to distinguish these races as species, yet, this cannot be done before a careful monographic study of the genus has been made.

Practical importance : This species is an active destroyer of timber; besides, it is poisonous, thus, in spite of its beauty, rather undesirable in the forests. It is possible that the yellow pigment can be extracted and used for stains in cytological laboratories.

SPECIES

O. olearius (D.C. ex Fr.) Sing. [Pleurotus, Gillet ; Clitocybe, R. Maire ; Clitocybe illudens (Schwein.) Sacc. ; Flammula phosphorea (Batt. ex) Quél.].

13. CLITOCYBE (Fr.) Quél.

Champ. Jura Vosges, p. 85. 1872-73, em.

Type species: Clitocybe infundibuliformis (Schaeffer ex Fr.) Quél.

Syn.: Agaricus tribus *Clitocybe* Fr., *Syst. Mycol.* 1: 78. 1821, p. p.
Omphalia Quél. *Enchir.*, p. 19, 1886, non (Pers. ex) S. F. Gray (1821), nec (Fr.) Quél. (1872-73).
Lepista (Fr.) W. G. Smith sensu Pat., *Hymen.* p. 96, 1887; nec non Roze, Gillet, Konrad & Maublanc (sect. *Eu-Lepista* Konr. & Maubl., *Icon. Sel.* **6**: 350. 1924-37) p. p., non W. G. Smith (1870).

Characters: Carpophores of strictly clitocyboid habit, often depressed or umbilicate in the center of the pileus with the lamellate hymenophore deeply decurrent; or adnate-subdecurrent; sometimes developing HCN; pileus dry or hygrophanous, very rarely viscid, pigmentless or colored, and then pigment usually intracellular and dissolved in the cell sap, dull colored (gray, umber, etc.), or green, or very frequently ochraceous, pinkish buff, cinnamon, fulvous chestnut color, etc.; epicutis little differentiated, consisting of a sericeous or subpubescent covering of repent or loosely interwoven filamentous hyphae; lamellae thin, often arcuate, white, concolorous with the pileus, or cream colored, often developing cyanic acid; spore print pure white, cream color, greenish, or pale sordid salmon color (but never pale vinaceous drab), in the latter case, the spores never rough, in general spore wall always smooth except in species with white spore print and with globose or subglobose spores; spore wall always nonamyloid, very thin; basidia normal, usually 4 spored, rarely 2 spored; cystidia none (rarely with very inconstant, inconspicuous and scattered pseudoparaphyses or cheilocystidia, very rarely with well developed, crowded cheilocystidia); hymenophoral trama regular or subregular, or subbilateral-subregular, never strongly intermixed nor completely irregular in the species studied, nor distinctly bilateral or inverse, always nonamyloid; stipe usually central, fibrous-fleshy or with cartilaginous rind, solid, or becoming hollow; context non reviving, fleshy soft, or soft fibrous in the pileus, never tough or leathery; hyphae with thin, rarely irregularly and slightly thickened walls, always with numerous clamp connections. On soil, in deep moss, on foliage and needles, on decayed wood and on charcoal, in and outside the woods, rarely on dung or in garden beds,

Development of the carpophores: Probably always gymnocarpous, but few data available (see Blizzard).

Area: Cosmopolitan.

Limits. Clitocybe is well delimited from all genera of this group and the *Tricholomatinae*; yet, the hiatus separating it from *Collybia*, *Lepista*, and *Tricholoma* is rather slight. The genus is also close to *Omphalotus*, *Hypsizygus*, *Pleurocybella*, *Omphalina*, and *Trogia*.

1) *Collybia.* At the level of the hygrophanous, smaller species, the difference in habit between *Clitocybe* and *Collybia* becomes rather small. On the other hand, there are such species in *Collybia* as *Collybia clusilis* and *C. vulgaris*, both in the characteristic dull colors of the hygrophanous Clitocybes, and with a very inconstant manner of gill attachment. However, the incrusting pigment of *Collybia vulgaris*, and the constantly collybioid habit of *C. clusilis* make it possible to draw a rather sharp line between the two genera.

2) *Lepista.* At the level of the section *Disciformes*, we find certain species that come extremely close to *Lepista*, especially in the *Inornatinae*. In these groups, the spore print tends to be slightly colored, and in some cases it is frankly sordid pink rather than cream color or greenish. However, if it is made clear that the species of *Lepista* must have both pinkish and rough spores, the generic distinction is still possible, inasmuch as the typical species of *Lepista*, in their habit, are rather like *Tricholoma* than *Clitocybe* [except for *L. subaequalis* (Britz.) Sing.], and, in fact, were also listed as such by Fries and the various authors following the Friesian scheme.

3) *Tricholoma.* Anatomically, there is hardly much difference between the sections *Leucorigida* and *Rigida* of *Tricholoma* on one hand and *Clitocybe*, sect. *Disciformes* on the other hand. However, the Tricholomas have a strong, distinct, and constant sinuate emargination where the lamellae join the stipe, a feature already emphasized by Fries, and never observed in *Clitocybe*. On the basis of the form of attachment of the lamellae, these two groups can be easily separated. This, however, is only true if such heterogeneous elements of both genera as the species of *Lyophyllum*, *Lepista*, *Leucopaxillus*, *Melanoleuca*, *Tricholomopsis*, etc. are first removed from *Clitocybe* and *Tricholoma*.

4) *Omphalotus.* As for the delimitation of that genus from *Clitocybe*, see under *Omphalotus*.

5) *Hypsizygus.* See under that genus.

6) *Pleurocybella.* This genus differs in more eccentric stipe than is

usual in *Clitocybe* (the stipe may be entirely absent as in the type species of *Pleurocybella*), and completely irregular, even somewhat intermixed hymenophoral trama, also in constantly epixylous habitat, and not clearly decurrent lamellae.

7) *Omphalina*. This genus has been separated from *Clitocybe*, in the past, by various standards. Fries emphasized cartilaginous stipe, a feature that is most arbitrary, and is often found in species that are not otherwise different from *Clitocybe*, even in such species that were actually inserted in *Clitocybe* by Fries himself. This difficulty arises especially at the level of the hygrophanous Clitocybes and the larger Omphalinas. Noting that the type species of *Omphalina* and the closely related species have no clamp connections, the author thought it possible to divide *Clitocybe* and *Omphalina* by this character (1942). However, this separation is not quite satisfactory because of the fact that some species of *Omphalina*, otherwise inseparable from the typical Omphalinas, have numerous clamp connections in all heterothallic forms. Nevertheless, there is a definite hiatus between these species and the species with cartilaginous stipe that are close to *Clitocybe*. The latter have regular or subregular trama, often with the outermost hyphae very slightly diverging toward the hymenium, with the walls of the hyphae thin, with the cuticle colored by an intracellular pigment that is never bright yellow or orange. In contrast to this, the true *Omphalinae*, even those with clamp connections, have bright yellow or orange pigment, or if the pigment is dull colored or some other color, it is a membrana pigment that often seemingly incrusts the hyphal wall and is not easily dissolved; the hymenophoral trama consists of very irregular hyphae which have a comparatively thick wall, and this in turn makes them appear somewhat opaque. Only in a few species, a central, narrow, regular mediostratum is visible, but usually, the hyphae of the hymenophoral trama are not arranged regularly. This separation is also that envisaged, as it seems, by the modern French authors, Kühner and Romagnesi.

8) *Trogia*. This genus differs from *Clitocybe* in reviving context and a pedestal at the base of the stipe. It is, in a manner of comparison, a *Clitocybe* with tough, reviving carpophores, and a *Collybia* with deeply decurrent lamellae. There is little danger that these two genera will ever be confused, or their hiatus be narrowed too much.

To sum up, we may say that *Clitocybe* is, though extremely close to some other genera of the *Clitocybeae*, always clearly separable

from them. Those who think, that nevertheless the hiatus between *Clitocybe* and these genera is too small, should consider the fact that the hiatus between these genera themselves, especially *Tricholoma* and *Lepista*, and *Tricholoma* and *Collybia*, are by no means more abrupt than the hiatus between these genera and *Clitocybe*. It would, therefore, follow that all these genera should, according to those who favor larger units, be combined into a single mammoth genus, comprising precisely those genera that were thus far strictly respected by the Fries-Saccardo school of thought — genera that, by their characters, answer to the Friesian scheme of macroscopical classification in a classical and almost perfect manner, by far better than the genera of other families where these same characters were schematically applied without regard for natural affinities. A tribus as rich in closely related forms as the *Clitocybeae*, evidently of recent origin, at least as far as its terminal branches are concerned, cannot be expected to form series interrupted by a hiatus comparable in value with the hiatus in a group such as the *Amaniteae* or certain Gastromycetes. If the genera are homogeneous, and their sequence reflecting their affinities, we have natural genera, whether the hiatus is more or less abrupt.

State of knowledge: Because of the scarcity of outstanding characters in this genus, usable for the distinction of species, and also because of the large number of species belonging here (about 200-300 species can now be considered as belonging in the genus *Clitocybe* — as emended in the present work — with reasonable certainty[34]), there is a great need for serious and comprehensive monographic work. Preliminary tests on only a few dozen species have demonstrated that chemical reactions such as those obtained with ferric sulphate, monomethylparamidophenol, and others, will be useful for the taxonomist. The constancy of the color of the spore print and the constancy of the measurements of the spores within certain limits should not be minimized. More attention should be given to the tropical and East asiatic species, not to mention those of the southern hemisphere.

Practical importance: A revision of the species of *Clitocybe* is the more desirable as some species of *Clitocybe* have an excellent record as bacteriostatics, some are good edible mushrooms, others are poisonous in a varying degree causing sickness with the characteristic muscarine syndrome. *C. Augeana*, belonging to a group where poison-

[34] 76 Species are indicated below.

-ous forms are common (*C. dealbata* and allied species), is especially interesting since it invades white mushroom cellars and is regarded as a « weed mushroom » by growers.

SPECIES

Subgenus I. **Eu-Clitocybe** Konr. & Maubl. (1924 37). Pileus more or less fleshy and hygrophanous or nonhygrophanous; if hygrophanous, rhizoid like pseudorhizas are present, or the odor of anise or *Collybia dryophila* is distinct, or the whole fruiting body is either practically pigment less or the pileus cinnamon-flesh color, or spores ellipsoid and smaller than 6 μ; spores either very small and globose and rough-echinulate, or with very thin, smooth wall; basidia usually small; spore print pure white or slightly colored; hyphae of the hymenophoral trama not vesiculosely widened; stipe fibrous-fleshy, rarely subcartilaginous.

Type species : C. infundibuliformis (Schaeff. ex Fr.) Quél.

Sect. 1. DISCIFORMES (Fr. ut sect. *Agarici*, trib. *Clitocybe*) Quél (1872 3). (sect. *Pseudoclitocybe* Vel. 1939, p. p.), Pileus becoming depressed in age but usually convex or flat at beginning maturity; young lamellae usually merely adnate, old lamellae often separable from the context of the pileus; spore print pure white, or slightly colored (e. gr. « cream » or « corn silk » to pl. IX, 1 3. M. & P.); cuticle of the pileus not hygrophanous except if the spore print is colored, and then only partially in some species.

Type species : C. nebularis (Batsch ex Fr.) Quél.

Subsect. Nebularinae Sing. (1948). Spores not fusoid, and not narrower than half their length (Q smaller than 2).

Type species : C. nebularis (Batsch ex Fr.) Quel.

C. nebularis (Batsch ex Fr.) Quél.; *C. alba* (Bat.) Sing. (C. nebularis var. alba Bat.); *C. clavipes* (Pers. ex Fr.) Quél.; *C. Trogii* (Fr.) Sacc.; *C. odora* (Bull. ex Fr.) Quel.; *C. Alexandri* (Gill.) Konrad (= ? C. Harperi Murr.).

Note : The spore print is white in *C. Alexandri* and *C. clavipes*, and colored in *C. nebularis*, *C. alba*, *C. odora*, and *C. Trogii*.

Subsect. Inornatinae Sing. (1948). Spores fusoid to ellipsoid oblong or subcylindric.

Type species : C. inornata (Sow. ex Fr.) Gill.

C. inornata (Sow. ex Fr.) Gill.; *C. Chuducae* R. Maire; *C. avellanea*

(Murr.) Sing. (Melanoleuca, Murr.); *C. avellaneialba* Murr.; *C. mexicana* Murr.; *C. lata* (Peck) Sing. (Tricholoma, Peck): perhaps also some species now considered as *Tricholoma*, see p. 224.

Sect. 2. **EULEPISTAE** (Konr. & Maubl. 1924 37) Sing. (1943). (= *Lepista*, sect. *Eu Lepista* Konr. & Maubl.). Spores globose or almost so, rough to finely echinulate, hyaline; pileus sometimes with hygrophanous spots, not otherwise hygrophanous; lamellae decurrent, often forked; spore print white or nearly so.

Type species: C. inversa (Scop. ex Fr.) Quél.

C. inversa (Scop. ex Fr.) Quél.; *C. gilva* (Pers. ex Fr.) Quél. sensu Gillet; Ricken; *C. lentiginosa* (Fr.) Gillet (*C. lenticulosa* Gillet); *C. subhirta* (Peck) Peck; *C. subconnexa* Murr.

Sect. 3. **INFUNDIBULIFORMES** (Fr. ut sect. *Agarici* trib. *Clitocybis*, 1821) Quél. 1872-73, em. Pileus soon depressed to infundibuliform, pale fulvous or pinkish buff, more rarely deeper chestnut or fuscous, never green, white, gray, or fuscous gray, never hygrophanous; lamellae deeply decurrent in all stages; stipe without « rhizoids »; spore print pure white or nearly so; spores cylindrical, ellipsoid, ovoid, or subglobose, always perfectly smooth under a good oil immersion lens.

Type species: C. infundibuliformis (Schaeff. ex Fr.) Quél.

C. sinopica (Fr.) Quél.; *C. Bresadoliana* Sing.; *C. altaica* Sing.; *C. Bresadolianoaffinis* Sing.; *C. subquamulosa* Sing.; *C. incilis* (Fr.) Quél. sensu Velen., Bres., Sing.; *C. infundibuliformis* (Schaeff. ex Fr.) Quél.; *C. splendens* (Pers. ex Fr.) Quél. sensu Bres., non Konr. & Maubl. (quae ad *Eulepistas* transferenda); *C. maxima* (Fl. Wett. ex Fr.) Quél.; *C. geotropa* (Bull. ex Fr.) Quél.; *C. calcarea* Velen.

Sect. 4. **VERNAE** Sing. (1943). Pileus reddish buff, buff, or fuscous gray, always abundantly pigmented, mostly hygrophanous; lamellae subdecurrent; base of the stipe with short white rhizomorphs that appear as « rhizoids »; spores perfectly smooth; carpophores often fruiting early in spring or late in fall, mostly under conifers.

Type species: C. rhizophora (Velen.) Josserand.

C. vermicularis (Fr.) Quél.; *C. rhizophora* (Velen.) Joss.; *C. autumnalis* Sing.

Sect. 5. **CANDICANTES** Quél. (1888 ut sect. gen. *Omphaliae*). Pileus either soon depressed or depressed only in age, mostly completely pigmentless or practically so, i.e. carpophores mainly white; if pigmented at all, the spores are smaller than 6 µ, or the odor of anise or *Collybia dryophila* is very distinct; pileus not hygropha-

nous, or more or less hygrophanous; if hygrophanous at all, the spores are smaller than 6 μ, or the odor of anise or *Collybia dryophila* is very distinct; spore print pure white or nearly so; spores globulose guttiform, more often more or less ellipsoid to ovoid, smooth.

Type species : *C. suaveolens* (Schum. ex Fr.) Quél.

C. washingtoniensis Murr.; *C. regularis* Peck; *C. obsoleta* (Batsch ex Fr.) Quél.; *C. Velenovskyi* Sing.; *C. suaveolens* (Schum. ex Fr.) Quél.; *C. fragrans* (Sow. ex Fr.) Quel.; *C. setiseda* (Schwein.) Sacc.; *C. subbulbipes* Murr.; *C. steppicola* Sing.; *C. Vasilierae* Sing.; *C. diatreta* (Fr.) Quél.; *C. angustissima* (Lasch) Quél.; *C. phyllophila* (Fr.) Quél. sensu Lange; *C. pithyophila* (Secr.) Gillet; *C. laricicola* Sing.; *C. catalaunica* Sing.; *C. leptoloma* (Peck) Peck; *C. monticola* Sing.; *C. ericetorum* (Bull. ex Fr.) Quél.; *C. tuba* (Fr.) Gillet; *C. catinus* (Fr.) Quel.; *C. adirondackensis* (Peck) Sacc.; *C. glutiniceps* A. H. Smith; *C. brumalis* (Fr.) Quél.; *C. griseifolia* Murr.; *C. subhygrophana* Sing.; *C. rivulosa* (Pers. ex Fr.) Quél.; *C. truncicola* (Peck) Sacc.; *C. Augeana* (Mont.) Sacc.; *C. dealbata* (Sow. ex Fr.) Gillet [11]; *C. olorina* (Fr.) Gillet; *C. Robinsoniae* Murr.; perhaps also *C. lignatilis* (Pers. ex Fr.) Karst. sensu Heim & Romagnesi, non sensu Kuhner.

Note : Several other species that seem to belong here have not been studied by the author, or if so, with insufficient data at hand. « *Omphalia* » *microspora* Bres. and « *Omphalia* » *Luffii* Mass. probably belong in this genus and this section, but they may be nanisms of other species. The same holds true for numerous species described by Velenovsky from Europe and by Peck and Murrill from North America.

Subgenus II. **Pseudolyophyllum** Sing. (1943). Pileus hygrophanous, rarely white or whitish or cinnamon flesh color when moist; spores smooth, comparatively not very small (larger than 5 μ in most species) unless they are subglobose, or the tramal hyphae inflated; basidia sometimes comparatively large; pigments dull (gray to fuscous gray, umber, blackish fuliginous, etc.); odor often farinaceous, not of anise; short, rhizoid like rhizomorphs at the base of the stipe none; hyphae of the hymenophoral trama equal or inflated; subhymenium not excessively broad; stipe fibrous-fleshy to subcartilaginous or with cartilaginous rind.

[11] The *C. dealbata* of C. H. Kauffman and some other American authors is actually *C. truncicola* Peck; *C. sudorifera* is *dealbata*, and *C. morbifera* Peck is another synonym.

Type species : *C. metachroa* (Fr.) Quél.

Sect. 6. **HYGROPHANAE** Quél. (ut sect. gen. *Omphaliae*, 1888). Spores 5-8 μ long, more or less ellipsoid; hyphae of the hymenophoral trama equal or nearly so; stipe not conspicuously cartilaginous; pileus rarely deeply umbilicate-infundibuliform.

Type species : *C. vibecina* (Fr.) Quél. sensu Ricken

C. expallens (Pers. ex Fr.) Quel. sensu Bres.; *C. vibecina* (Fr.) Quél. sensu Ricken; *C. Langei* Sing. (C. vibecina sensu Lange); *C. metachroa* (Fr.) Quel.; *C. albocinerea* Rea; *C. concava* (Scop. ex Fr.) Gillet; *C. fuliginelpes* Metrod; *C. pseudoobbata* Lange; *C. lixivia* (Fr.) Sing. sensu Sing.; probably also *C. Imaiana* Sing.

Sect. 7. **UMBILICATAE** Sing. [subgen. *Omphalina* (Quél.) Sing. 1943 *non Omphalina* (Quel.) 1886] Spores rather large (larger than 5.5 μ); hyphae of the hymenophoral trama equal or nearly so, none of them conspicuously inflated; stipe with cartilaginous rind, or entirely cartilaginous; pileus deeply umbilicate, and eventually strongly infundibuliform.

Type species : *C. umbilicata* (Fr.) Sing.

C. umbilicata (Schaeff. ex Fr.) Sing. (Omphalia, Quél.); *C. strombodes* (Berk. & Mont.) Sing. (Omphalia, Sacc.); also, probably the so-called « *Omphaliae* » : *O. striaepilea* (Fr.) Gillet; *O. leucophylla* (A. & S. ex Fr.) Gillet; *O. litua* (Fr.) Gillet; possibly the echinosporous *O. asterospora* Lange. Close to *C. strombodes* is *Clitocybe xanthophylla* Bres. which has clamp connections but whose trama has not been studied recently, and may be of the *Omphalina* type.

Sect. 8. **BULLULIFERAE** Sing. (1943). Differing from the preceding section in very small ellipsoid spores, and inflated hyphae in the cuticle and the hymenophoral trama; these inflated hyphae reach a diameter nine times as large as the non-inflated portions of hyphae.

Type species : *C. Kuehneri* Sing.

C. hydrogramma (Bull. ex Fr.) Sing. (Omphalia, Quél.; Clitocybe Kuehneri Sing.).

Note. The *C. gallinacea* described by Kühner is undoubtedly not the *C. gallinacea* of Fries and therefore was named *C. Kuehneri* by Singer (1943). However, Romagnesi quotes Malençon as claiming that the *C. gallinacea* of the Parisian mycologists is *Omphalia hydrogramma* (Bul. ex Fr.) Quél., and an anatomical check on available European specimens of *C. hydrogramma* shows that they actually have the inflated elements in the trama, characteristic for this section.

Sect. 9. **DITOPAE** Sing. (1948). Spores smaller than or just reaching 5 μ in diameter, subglobose or very broadly ellipsoid in the same print.

Type species : *C. ditopa* (Fr.) Gillet [40].

C. ditopa (Fr.) Gillet.

Sect. 10. **IGNOBILES** Sing. (1948). Spores larger than 9 μ in diameter, ellipsoid; habit that of an omphalioid *Marasmiellus* or *Delicatula* (stipe up to 1 mm thick); pigment none; pileus strongly hygrophanous.

Type species : Omphalia ignobilis Josserand.

C. ignobilis (Josserand) Sing. (Omphalia, Josserand; Mycena, Kühner).

14. LEPISTA (Fr.) W. G. Smith

Clavis Agar., p. 26. 1870

Type species : Paxillus lepista Fr. [= *Lepista subaequalis* (Britz.) Sing.].

Syn. : Paxillus, trib. *Lepista*, Fr., *Epicr.*, p. 315, 1838.
Rhodopaxillus R. Maire, *Ann. Myc.* 11 : 337. 1913 (type : *R. panaeolus*).

Characters : Pileus hygrophanous, subhygrophanous, or nonhygrophanous; hymenophore lamellate; lamellae emarginate-sinuate as in *Tricholoma*, or more rarely plainly decurrent, often separable from the context of the pileus from which they are divided by a watery or subcartilaginous line or zone; stipe usually central and fibrous-fleshy; context never tough or reviving; carpophores sometimes aggregated into large cespitose masses, or very densely gregarious in circles (« fairy ring »); spores rather small and coarsely to very minutely roughened in outline, nonamyloid, thin-walled, sometimes part of the spores smooth but always a certain percentage more or less rough, ellipsoid, or short-ellipsoid, or ovoid, rarely ellipsoid-oblong, hyaline; very pale sordid pink to cream pink in mass (on white paper), e. gr. Seguy 200 in *L. sordida*; basidia normal in every regard; cystidia of any sort absent; hymenophoral trama regular or subregular, all hyphae nonamyloid, with numerous clamp connections; epicutis little differentiated. On the soil, on roadsides, in the woods, on meadows, in parks, in steppes, and deserts,

[40] The specific epithet is often incorrectly spelled *ditopoda*. Di-topus, however, has nothing to do with pous, podos (foot), but means « of two shapes ».

on manure heaps in the garden, on compost heaps, etc., ordinarily not on wood.

Development of the carpophores : Hymenium of external origin, carpophores gymnocarpous (Kühner).

Area : Probably cosmopolitan.

Limits : The rule indicated under *Clitocybe*, leaving all species with smooth spores in *Clitocybe*, and those with colored spore print and rough spore wall in *Lepista*, will take care of the present needs of the taxonomist. There is, however, no guarantee that the line of separation between the two genera will be permanently on this level. After a monograph of *Clitocybe* will accumulate more data, it is possible that some species of *Clitocybe* will eventually be shifted over into *Lepista*. The same is perhaps to be expected in regard to *Tricholoma*. Metrod (1939) has already transferred *Tricholoma irinum* to *Rhodopaxillus*, i. e. to *Lepista*, claiming that the spores are rough in that species. More detailed monographic work will probably show that there is a smooth spored species (which the author collected in Leningrad but from which he did not obtain a spore print) that might be called *Tricholoma irinum*, and a rough spored species (the spores are extremely finely roughened, and not in all spores at that) with a pale sordid pink spore print on pure white paper. This latter species may be the one Metrod has examined, but it is considered as a different species in the present treatment (*L. Rickenii* Sing.). Nevertheless, this somewhat complicated situation shows clearly enough that the limits between *Tricholoma* and *Lepista* are by no means very sharp. In some of our previous papers, we have followed R. Maire in including in this genus such species as *Rhodopaxillus truncatus* (Fr.) Maire and *R. popinalis* (Fr.) Kühner & Maire, on the mistaken assumption that these species combine all the essential characters of *Lepista*. Yet, these species, — our sections *Decurrentes* Konr. & Maubl. and *Nitellini* (Konrad & Maubl.) of *Rhodopaxillus* — have no clamp connections, and it is improbable that they are actually closely related to *Lepista*. They approach very closely some groups of the genus *Rhodophyllus*, and also *Clitopilus*, both of the family *Rhodophyllaceae*. Since they differ from *Rhodocybe* only in the absence of pseudocystidia, the author now combines these sections with *Rhodocybe*, and transfers the latter genus to the *Rhodophyllaceae*. According to Kühner (1945), the species here considered as true *Lepistae*, have uninucleate spores, and those transferred to *Rhodocybe* have binucleate spores. The incrusting pigment, found in some of

the Rhodocybes, is also present in many *Rhodophylli*, but not in *Lepista*.

State of knowledge: The more extended use of chemical characters and a more careful observation of the variability of the degree of roughness of the spores and the shades of pink observed in the spore print of the different species will perhaps add to our knowledge of this thus far rather «monotonous» genus, now consisting of 15 species.

Practical importance: Lepista contains some of the most valuable edible mushrooms, and some of the most promising bacteriostatic organisms among the *Agaricales*. The best known edible species are: *L. nuda* (also grown in France, and often in the markets), *L. personata, L. sordida, L. Rickenii, L. caespitosa, L. caffrorum* (one of the most important edible mushrooms of the natives of South Africa), *L. lactescens* (one of the most widely used edible mushrooms in Indo China), *L. praemagna*.

SPECIES

Sect. 1. **PANAEOLAE** Sing. ut sect. gen. *Rhodopaxilli* (1943). Stipe more or less white or whitish; habit not always tricholomatoid.

Type species: L. panaeola (Fr.) Karst. (= *L. luscina*).

L. caffrorum (Kalchbr. & McOvan) Sing. (Tricholoma, Kalchbr. & McOvan; Rhodopaxillus, Sing.); *L. lactescens* (Pat.) Sing. (Tricholoma, Pat.; Rhodopaxillus, Sing.); *L. praemagna* (Murr. sensu Overholts) Sing. (Melanoleuca, Murr. †; Tricholoma, Murr. sensu Overholts); *L. caespitosa* (Bres. p. p.) Sing. (Tricholoma panaeolus var. caespitosus Bres. p. p.; Rhodopaxillus caespitosus Sing.); *L. luscina* (Fr.) Sing. [Clitocybe, Karst.; Tricholoma, Lund. & Nannf.; Tricholoma panaeolum (Fr.) Quél.; Lepista, Karst.; Rhodopaxillus, R. Maire; Agaricus panaeolus * calceolus Fr.; Rhodopaxillus nimbatus (Batsch ex Secr.) Konr. & Maubl.]; *L. Harperi* (Murr.) Sing. (Melanoleuca, Murr.); *L. subaequalis* (Britz.) Sing. (Agaricus, Britz.; Tricholoma, Sacc.; Paxillus lepista Fr. sensu Bres. non Ricken; Rhodopaxillus, Sing.); *L. Rickenii* Sing. (Tricholoma panaeolus sensu Ricken non al.); *L. glabella* (Speg.) Sing. (Clitopilus, Speg.; Lepista Westii Murr.); *L. panaeoliformis* Murr. Probably also *Melanoleuca Olesonii* Murr. and *M. rudericola* Murr. [6]).

[6] In the first species, the exact color of the spores, and in the second, the presence of clamp connections has not been verified.

Sect. 2. **GENUINAE** Konr. & Maubl. ut sect. gen. *Rhodopaxilli* (1924-37). Stipe more or less bluish lilac, violet, pale blue, or purplish colored when young and fresh; habit decidedly tricholomatoid in most normally developed carpophores.

Type species : *L. nuda* (Bull. ex Fr.) W. G. Smith.

L. nuda (Bull. ex Fr.) W. G. Smith (Tricholoma, Quél.; Rhodopaxillus, R. Maire) with var. *typica*, var. *tridentina* (Sing. ut Rhodopaxillus) Sing., var. *violaceofuscidula* (Sing. ut Rhodopaxillus) Sing., var. *lilacina* (Quel. ut Gyrophila) Sing.; *L. personata* (Fr. ex Fr.) W. G. Smith (Tricholoma, Quél.; Rhodopaxillus, Sing.); *L. glaucocana* (Bres.) Sing. (Tricholoma, Bres.; Rhodopaxillus, Metrod); *L. sordida* (Fr.) Sing. (Tricholoma, Quel.; Rhodopaxillus, R. Maire); either here, or in preceding section: *L. argentina* (Speg.) Sing. (Tricholoma, Speg.).

KEY TO THE SPECIES

A. Species without any bluish, lilac, violet, livid colors on the stipe and the lamellae (but lamellae becoming more or less dirty pink in age from the spores).

B. Pileus white, often with pale dirty buff or pale brownish center.

C. Outside of the forested areas, more rarely under trees (in parks, on lawns, etc.).

D. Carpophores very large (pileus 50-300 mm). North America, East Asia, South Africa.

E. Spores slightly rough.

F. Carpophores somewhat « lactescent ». Indo-China. *L. lactescens*

F. Not so. North America. *L. praemagna*

E. Spores strongly warty. South Africa. *L. cafforum*

D. Carpophores medium sized to rather large (pileus 40-80 mm broad). Europe, North Africa, and northern Asia south to central Asia. *L. caespitosa*

C. In dense coniferous and mixed woods in Europe and Asia, also in North America; rather rare. *L. subaequalis*

B. Pileus not white, not even prevalently white, and not white in dried specimens.

G. Pileus horn gray to pale grayish fuscous in the center, almost whitish at the extreme margin which is pruinose, pale gray in dried condition, more or less watery-guttate where the pruina is absent, the guttulae sometimes regularly arranged in obscure concentric zones, margin radially sulcate or smooth; carpophores fasciculately-seriate in « fairy rings » in Europe, North Africa, and North America. *L. luscina*

G. Colors different, or not combining the above characters.

H. Pileus smoky-umbrinous when moist, alutaceous when dry

California, perhaps also farther south (in that case cf. *L. argentina*). *L. Harperi*

H. Pileus not so colored. Eastern United States, Europe, or South America.

I. Pileus uniformly dark avellaneous with minute concolorous tufts of fibrils more persistent on the disc; spores very distinctly warty; odor and taste mild; on leafmold in Florida. *L. panaeoliformis*

I. Pileus glabrous except for the initially white-pubescent margin; spores either very slightly rough, or strongly warty, odor often acid; taste often slightly bitterish.

J. Spores slightly rough (some spores smooth); pileus « Havana » (Séguy 131) taste slightly bitterish in fresh condition; in boreal regions of Europe on pastures, meadows, and among scattered trees (coniferous and mixed stands). *L. Rickenii*

J. Spores almost subangular-warty; pileus « Buckthorn br. » to « honey, Middle Stone » taste mild; in hammocks in Florida and in Southern Brazil, also in Argentina. *L. glabella*

A. Lamellae or stipe with some bluish, lilac, violet, or livid tones.

K. Pileus rather pale colored; violet or lilac colors confined to the stipe; Europe. *L. personata*

K. Not so.

L. Colors rather sordid; pileus distinctly hygrophanous; medium sized species, almost cosmopolitan. *L. sordida*, *L. argentina*

L. Not so: colors rather bright or deep at least in youth; pileus not distinctly hygrophanous, except partially so in age; medium sized to large carpophores.

M. Pileus glauco-caesious or grayish lilac, in age becoming grayish; lamellae caesious-violet, stipe concolorous with the pileus; odor strong, almost farinaceous, in coniferous woods, Europe. *L. glaucocana*

M. Not combining these characters; widely distributed. *L. nuda*

15. TRICHOLOMOPSIS Sing.

Schweiz. Zeitschr. Pilzk. **17**: 13 [reprint pagination] 1939.

Type species: Tricholomopsis rutilans (Schaeff. ex Fr.) Sing.

Characters: Carpophores with tricholomatoid habit, more rarely clitocyboid, or almost pleurotoid because of the somewhat eccentric stipe observed in certain species; well pigmented with an intracellular pigment, at least the cuticle which is either bright colored (and then sometimes with dark-brown, fuscous, blackish squamulae on top of the pigmented surface of the pileus, and the lamellae and

stipe often colored with the same bright (usually yellow) pigment), or only the cuticle of the pileus (dull) colored; pileus more or less fleshy, not infundibuliform, more or less squamulose or fibrillose in all species, the cuticle little differentiated except for the terminal member of the hyphae that make up the fibrils; these terminal hyphae often slightly dermatocystidia-like and sometimes filled with a colored cell sap; hymenophore lamellate; lamellae yellowish or white, emarginate-sinuate as in *Tricholoma*, or adnate to somewhat decurrent as in *Clitocybe*, or merely adnexed as in *Collybia*; spore print pure white (or nearly so) on white paper; spores ellipsoid to globose, with thin, later sometimes slightly thickened, simple walls which are smooth, nonamyloid (yellowish in iodine), or very slightly pseudoamyloid (i. e. a minority of overmature spores, i. e. spores that have rested on the hymenophore for a long time, becoming palest brownish in iodine); basidia normal in all regards; cystidia none on the sides of the lamellae; but cheilocystidia very prominent on the edges of the lamellae, large to extremely voluminous but with thin walls and therefore soon collapsing to a degree that in dried material they may escape the attention of the observer; hymenophoral trama regular or subregular, consisting of rather long, sometimes even voluminous hyphae which are strongly interwoven to subparallel; stipe central or somewhat eccentric, fibrous-fleshy, solid or stuffed, sooner or later becoming hollow, but never cartilaginous-tubulose; all hypae nonamyloid, with numerous clamp connections. On rather fresh and on very decayed wood.

Development of the carpophores: Unknown.

Area: Probably nearly cosmopolitan.

Limits: The conspicuous cheilocystidia distinguish this genus well enough from all other genera of the *Clitocybinae*, and the constant presence of clamp connections distinguishes it from the *Tricholomatinae*. Some may find it tempting to compare this genus with the *Cystodermateae* (*Agaricaceae*); but that group has a much more differentiated epicutis which is either hymeniform or an epithelium, or it has cystidia on the sides of the lamellae. The affinity of *Cystoderma* and *Tricholomopsis* is hardly probable in the light of the recent cytological studies by R. Kühner (1945) who finds uninucleate spores in *Tricholomopsis rutilans*, and binucleate spore in the Cystodermas.

State of knowledge: The delimitation of certain species or forms within certain stirpes is not yet settled. Fourteen species are known

at present to belong in the genus *Tricholomopsis* but some of them have sometimes been considered as varieties of other species of the same genus; two have not been validly described.

Practical importance: Tricholomopsis appears to be a source of bacteriostatic substances, as promising as *Lepista.*

SPECIES

Sect. 1. **RUTILANTES** Sing. (1943). Pileus with deep carmine, light red, yellow, olive, violet livid, rusty brown, or blackish fuscous fibrils, or scales; lamellae yellow, livid or white.

Type species: T. rutilans (Schaeff. ex Fr.) Sing.

T. rutilans (Schaeff. ex Fr.) Sing. (Tricholoma, Quél.); *T. variegata* (Scop. ex Fr.) Sing. (Tricholoma, Gillet; Gyrophila rutilans var. variegata Quél.); *T. decora* (Fr.) Sing. (Clitocybe, Gillet; Pleurotus, Sacc.); *T. sulphureoides* (Peck) Sing) Pleurotus, Sacc.); *T. ornata* (Fr.) Sing. (Pleurotus, Sacc.); *T. fimbriatophylla* (Kauffm.) Sing. (Hygrophorus, Kauffm.); *T. flavissima* (A. H. Smith) Sing. (Clitocybe, A. H. Smith); *T. flavescens* (Peck) Sing. (Tricholoma, Sacc.); *T. formosa* (Murr.) Sing. (Cortinellus, Murr.); and a violet colored species from Florida *T. totilivida* (Murr. *ined.*); also *T. intermedia* Sing. *ad int.* (if independent).

Sect. 2. **PLATYPHYLLAE** Sing. (1943). Pileus dirty dull colored; lamellae wite.

Type species: T. platyphylla (Pers. ex Fr.) Sing.

T. platyphylla (Pers. ex Fr.) Sing. (Collybia, Quél.; Collybia grammocephala (Bull. ex, Quél.); *T. radicata* (Peck) Sing. (Tricholoma, Peck); *T. sececifolia* (Murr.) Sing. (Melanoleuca, Murr.).

KEY TO THE SPECIES

A. Lamellae yellowish or livid-lilac.
  B. Lamellae yellowish.
    C. Cheilocystidia filamentous, 40-200 × 3-5μ, subgelatinous ... *T. fimbriatophylla*, *T. flavissima*
    C. Cheilocystidia not filamentous, 4.5-30μ thick.
      D. Pileus with some red or reddish. Circumpolar species ... *T. rutilans*, *T. variegata*
      D. Pileus without any reddish tones.
        E. Lamellae narrow: less than one fifth of the radius of the pileus broad
          F. Pileus scaly.

G. Pileus with smooth, entire margin, with olive-fuliginous scales, obtuse or subumbonate on the disc ; spores (at least some of them) larger than 6.5 × 5.2μ; on pine, spruce, fir, Douglas fir, hemlock. Circumpolar. *T. decora*

G. Pileus with crenate-sulcate margin, umbonate, with fuscous-ferruginous scales ; spores 6-6.5 × 4-5.2μ ; on larch ; Altai. *T. intermedia ined.*

F. Pileus fibrillose-rimose ; North America. *T. flavescens*

E. Lamellae broader than indicated above.

H. Pileus umbonate, with not very distinct fuliginous scales which are fugacious, its diameter smaller than the length of the stipe ; on *Tsuga* and *Thuja*, in North America. *T. sulphureoides*

H. Pileus obtuse or subumbonate, with ferruginous or subconcolorous scales, its diameter larger than the stipe. Circumpolar. *T. ornata*

B. Lamellae not yellowish but livid. *T. lutilurida*, ined.

A. Lamellae white, later in one species becoming « sayal brown » or « ochraceous tawny » (R.).

I. Pileus cinnamon-bracceous to tawny to chestnut-ferruginous ; stipe usually at least partly concolorous. *T. formosa*

I. Pileus dull colored, gray, umber gray, grayish avellaneous, etc. ; stipe usually white.

J. Spores larger than 8.5μ ; pileus 120-200 mm broad, often squamulose ; odor and taste farinaceous. North America. *T. sererdifolia*

J. Spores smaller than 8.5μ, pileus often smaller than 120 mm, innately subsquamulose or rather fibrillose.

K. Spores 7-8.3 × 5.8-7.5μ ; base of the stipe attached to white rhizomorphs which connect the carpophores with the woody substratum. *T. platyphylla*

K. Spores 6-7 × 3.5-5μ ; base of the stipe distinctly projecting into a pseudorrhiza and thus connected with the buried substratum. *T. radicata*

16. COLLYBIA (Fr.) Quel.

Champ. Jura Vosges, p. 92. 1872-73, em.

Type species : *Collybia dryophila* (Bull. ex Fr.) Quel.

Syn. *Agaricus*, tribus *Collybia* Fr., *Syst. Mycol.* 1 : 129. 1821.

Sclerostilbum Povah, *Mycologia* 24 : 242. 1932 (imperfect form of *Collybia*, conf. Lütjeharms, in *Flora Batava*, 1936).

Dictyoploca (Mont. ut tribus nom. subnud.) Heim, *Rev. Myc.* 10 : 25. 1945.

Rhodocollybia Sing., *Schweiz. Zeitschr. Pilzk.* 17 : 15 (reprint pagination) 1939.

Characters : Carpophores strictly collybioid to marasmioid in habit, i. e. lamellae not distinctly decurrent but adnexed to subfree,

or sinuate to emarginate, or planely adnate; margin initially usually incurved; pileus not conico-campanulate but convex to flat, sometimes somewhat depressed but not strongly umbilicate in most species; stipe thin and rather tough to very tough string-like, more rarely somewhat thicker but then distinctly fibrous-toughish and soon becoming hollow; pileus without strongly differentiated epicutis, i. e. no sphaerocysts (epithelium), erect elements in palisade (trichodermial palisade, hymeniform layer), nor even any kind of modified hyphae (bross cells, diverticulate hyphae, dichophyses, etc.) present, the cuticle usually consisting of a denser layer of intricately interwoven, or repent, subparallel to parallel hyphae which are then radially arranged; hymenophore lamellate, often developing cyanic acid; hymenophoral trama regular or subregular (i. e. hyphae often very strongly interwoven), consisting of rather thin filamentous hyphae; basidia normal in all respects, rather small; basidioles fusoid; cheilocystidia absent, or present, and then often inconspicuous and appearing on mature specimens, directly from the hyphae of the trama; other cystidia none; spores from globose to ellipsoid to ovoid to fusoid to cylindric to claviform-oblong, with thin, smooth, nonamyloid walls, with or without suprahilar depression; spore print pure white, pale cream color, or often cream pink (Seguy 200, Crawshay D, Ridgway's «seashell pink»); stipe sometimes developing from sclerotia, sometimes forming conidia on the covering layer, smooth or longitudinally striate to sulcate, glabrous, pruinate, or velvety; pseudorhiza often present; context fleshy-tough or fleshy-fibrous, or sometimes plainly tough and reviving after the carpophores have dried out in situ, consisting of thin or thick walled hyphae, sometimes both thin and thick walled hyphae in one carpophore, the hyphae pigmented in many forms, the pigment either intercellular or membranal or intracellular, the hyphal walls never amyloid, all hyphae with clamp connections; gloeo-vessels none; latex none; taste mild or peppery; odor none, or characteristically of sauerkraut, of HCN (*Collybia dryophila*), or of dried celeriac, or garlic. On the soil, on needles or foliage or fungi decaying on the ground, or among deep moss, on decaying or rather fresh wood, often on humus in ruderate places, on lawns, in gardens, etc.

Development of the carpophores: C. tuberosa is gymnocarpous according to Moss and Reijnders.

Area: Cosmopolitan.

Limits: Species with distinctly decurrent lamellae do not belong

to *Collybia*, even though the characters of the stipe may fit in the diagnosis of *Collybia*. Species with rough spores do not belong in this genus but, if the spore print is pink, rather in *Lepista*. However, there is no doubt that the species with pinkish spore print in *Collybia* come rather close to *Lepista*; they can be distinguished by their more collybioid habit, the tougher stipe, the smooth spores, and the odor.

The genus *Collybia* was formerly a completely artificial group, poorly delimited from *Marasmius*, *Marasmiellus*, and not at all distinguished from *Oudemansiella*, *Xerula*, *Flammulina*, *Tricholomopsis*, *Micromphale*, and often confused with the group of genera that was then incorporated in *Mycena* and *Omphalia*. The characters of the epicutis clearly separate *Collybia* from nearly all species of the *Hemimyceneae* except *Lactocollybia* which has a latex, or pseudocystidia (gloeocystidia) or gloeo vessels; this made it possible to revise the limits of *Collybia* against *Marasmius* and allied genera. One species of *Collybia* was then transferred to *Tricholomopsis* because of the more conspicuous cheilocystidia, and more tricholomatoid habit, and the absence of affinities in *Collybia*. *Micromphale* was never part of *Collybia*, yet, because of the repent, smooth hyphae of the epicutis undoubtedly comes closer to this genus than *Marasmius*. The presence of black rhizomorphs, a strongly gelatinized cuticle, or a horsehair-like stipe, are characters found only in *Micromphale*. Nevertheless, *Micromphale* is merely a more differentiated and adapted group of *Collybia*, one step on the way toward *Marasmiellus* and *Marasmius*; this is especially true for the insititious stipe, a character often found in the *Hemimyceneae*, and therefore here used as the main distinguishing character from *Collybia*.

As for the delimitation of *Collybia* against *Clitocybe*, see there. As for the limits of sect. *Cirrhatae* with *Marasmiellus*, see footnote on p. 202.

State of knowledge: Collybia is a comparatively well-known genus, yet, a monograph would probably bring out a clearer picture of the various species belonging here. Certain groups, such as that of *Collybia fuscopurpurea* (and that whole section) and that of *C. maculata* (and that whole section) are badly in need of revision. The exact color of the spore print, the exact arrangement of the cuticular hyphae and the macroscopical characters (lamellae, color), microscopical characters such as spore size and shape, localization of the pigments, and finally chemical characters will be helpful. The odors are rather

characteristic in this genus, and so is the taste of the context in at least two species. The author admits only 33 species in the enumeration of the species but many more will eventually remain in or be transferred to *Collybia,* and many more, mainly tropical species (some with branching stipes, others with minute spores) are still undescribed, or in need of additional observations.

Practical importance : Negligible according to the available data.

SPECIES

Sect. 1. **FARINOLENTES** Sing. (1948). Stipe smooth, glabrous; spore print white; hyphae of the cuticle incrusted with a dull colored pigment; flesh not reviving, slowly darkening with Fe SO_4.

Type species : C. vulgaris Sing.

C. vulgaris Sing.; *C. clusilis* (Fr.) Gillet sensu Konr. & Josserand.

Sect. 2. **LEVIPEDES** (Fr.) Quél. (1872-73). Stipe smooth and glabrous, except for the basal tomentum; spore print white, rarely palest creamy white, especially after desiccation, not cream pink when fresh; pileus rather bright colored; lamellae normally not strongly anastomosing.

Type species : C. dryophila (Bull. ex Fr.) Quél.

Stirps **Dryophila** (Pigment not behaving like an indicator).

C. dryophila (Bull. ex Fr.) Quél.; *C. acervata* (Fr.) Gillet.

Stirps **Iocephala** (Pigment turning pink with acids, violet with alkalis).

C. iocephala (Berk. & Curt.) Sing. (Marasmius, Berk. & Curt.).

Sect. 3. **DICTYOPLOCAE** (Mont. ut tribu, nom. subnud.) Sing. Stipe very slightly sulculate-striatulate, almost smooth, glabrous; spore print creamy white when fresh but becoming pinkish cream in the herbarium; pileus white to violet; lamellae slightly to mostly strongly venose-anastomosing.

Type species : C. plectophylla (Mont.) Sing.

C. plectophylla (Mont.) Sing. (*Marasmius,* Mont.).

Sect. 4. **STRIIPEDES** (Fr. ut sect. tribus *Collybiae*) Quél. (1872-73). Stipe often rather thick, more or less longitudinally striate or sulcate; spore print more or less cream pink; pseudorrhiza sometimes present.

Type species : C. fusipes (Bull. ex Fr.) Quél.

Stirps Butyracea (Pseudorrhiza none or little developed; pileus

rather thin; cuticle somewhat opimous; odor of cyanic acid or none).

C. butyracea (Bull. ex Fr.) Quél. (including f. *asema* (Fr.) Sing.; also *C. albistricta* (Murr.) Murr. (Gymnopus mammillatus Murr.) if not specifically identical with the preceding species.

Stirps Fusipes (Perennial pseudorrhiza present; growing on the base of trees).

C. fusipes (Bull. ex Fr.) Quél. [C. lancipes (Fr.) Gillet]; here probably also *C. subsulcatipes* A. H. Smith.

Stirps Maculata (Pseudorrhiza present or absent, context of the pileus rather thick; cuticle dry; odor of celeriac, or none).

C. maculata (A. & S. ex Fr.) Quél.; *C. pinicola* (Murr.) Sing. (Melanoleuca, Murr.); *C. collybiiformis* (Murr.) Sing. (Melanoleuca, Murr.) *C. distorta* (Fr.) Quél; *C. margarita* (Murr.) Sing. (Melanoleuca, Murr.); *C. Murrilliana* Sing. (Melanoleuca maculata Murr.; ? C. maculata var. immaculata (Cooke) Sacc.); *C. Westii* (Murr.) Sing. (Melanoleuca, Murr.); also the following plants which are closely related and perhaps not all specifically different: *C. maculata* var. *immutabilis* A. H. Smith, *C. leucocephaloides* (Peck) Sing. (*Tricholoma*, Peck) and *Melanoleuca* (non *Collybia*) *unakensis* Murr.; probably also in this stirps: *C. bakerensis* A. H. Smith.

Sect. 5. **VESTIPEDES** (Fr.) Quél. (1872-73), em. (= *Marasmius*, sect. *Peronati* Kühner 1934). Stipe neither glabrous nor sulcate, entirely villous or tomentose or strigose; spore print pure white to pale flesh color (unknown in several species).

Type species: Collybia confluens (Pers. ex Fr.) Quél.[44].

C. peronata (Bolt. ex Fr.) Sing. (Marasmius, Fr.); *C. cylindrospora* Kauffm.; *C. confluens* (Pers. ex Fr.) Quél. (C. hariolorum (D. C. ex Fr.) Quél. 1872; Marasmius, Quél. 1888); *C. ingrata* (Schum. ex Fr.) Quél.; *C. porrea* (Pers. ex Fr.) Sing. (Marasmius, Fr.); *C. Cauretii* (Kühner) Sing. (Marasmius, Kühn.); *C. impudica* (Fr.) Sing. (Marasmius, Fr.); *C. fuscopurpurea* (Pers. ex Fr.) Sing. (Marasmius, Fr.); *C. putilla* (Fr.) Sing. (Marasmius, Fr.); *C. umbonatella* Sing. (Marasmius umbonatus Peck); *C. gilva* (Pat.) Sing. (Marasmius, Pat.); *C. spongiosa* (Berk. & Curt.) Sing. (Marasmius, B. & C.; Marasmius semihirtipes Peck; Marasmius semisquarrosus Berk. & Cooke.; *C. alkalivirens* Sing.; *C. collybioides* (Speg.) Sing. (Clitocybe, Speg.).

Sect. 6. **CIRRHATAE** Sing. (1943). Stipe not sulcate, finely prui-

[44] This section may not be quite homogeneous but rather composed of two or more elements which are here treated as a single group

nate pubescent, or with conidiophores; pileus white or whitish, in moist condition at least on the margin, very thin fleshy or membranaceous; stipe racemose, and/or rising from a sclerotium, more rarely neither racemose nor rising from a sclerotium; cheilocystidia none, or very inconspicuous. Frequently on decaying *Basidiomycetes*.

Type species: C. cirrhata (Schum. ex Fr.) Quél.) [63].

C. cirrhata (Schum. ex Fr.) Quél.; *C. Cookei* (Bres.) J. D. Arnold; *C. tuberosa* (Bull. ex Fr.) Quél.; *C. racemosa* (Pers. ex Fr.) Quél. (Sclerostilbum septentrionale Povah, sclerotial and conidial form).

KEY TO THE SPECIES

Unfortunately, there is no satisfactory key to the species of this genus. When older taxonomic works are consulted, care should be taken not to omit the species then considered as *Marasmius* instead of *Collybia*.

17. PLEUROCYBELLA Sing.

Mycologia **39**: 81. 1947.

Type species: Pleurocybella porrigens (Pers. ex Fr.) Sing.

Characters: Pigment none, or almost none; carpophores pleurotoid; pileus comparatively thin; cuticle little differentiated; lamellae adnato subdecurrent or attenuate concurrent, often developing cyanic acid; spore print white; spores hyaline, globose or subglobose or more or less ellipsoid, thin-walled, nonamyloid, small; basidia normal in all regards; cystidia none of any kind; hymenophoral trama irregular, almost intermixed with or without a slight axillar trend, consisting of thin-walled, later thick walled (0.5-1.0 μ) hyphae which sometimes break through the hymenial layer, and assume the shape of hymenial hairs in old specimens; stipe none, or more or less eccentric; veil none; context thin fleshy, slightly tough; trama nonamyloid, non gelatinous, consisting of hyphae with clamp connections and somewhat thickened walls in old specimens. On wood.

Development of the carpophores: Unknown.

[63] The author has formerly considered *Marasmius candidus* (Bolt. ex Fr.) Fr. as a species of *Collybia*, sect. *Cirrhatae*. It appears to be preferable, however, to transfer it to *Marasmiellus* because of its similarity with *Marasmiellus tricolor* (A. & S. ex Fr.) Sing., and because of the presence, on the stipe, of some diverticulate elements, also because of the cheilocystidia which are not inconspicuous at all, and the distant lamellae which are rather unusual in this section of *Collybia*.

Area : Boreal and temperate.

Limits : This genus is most closely related to *Clitocybe, Hypsizygus*, and *Nothopanus*. It differs from the first two genera in the extremely irregular trama, and, in addition, from *Clitocybe* in habit and (usually) in habitat, and from *Hypsizygus* in persistently thinwalled spores and narrower lamellae which are either adnato-decurrent or attenuate-concurrent.

State of knowledge : Only one species is completely known, the other species, thought to belong here, is reasonably well known, well enough, in the author's opinion to be inserted in this genus in spite of the fact that it differs strongly from the type species in habit. It may be expected that several more species will eventually be found to belong in *Pleurocybella*. In the group of *Pleurotus* sensu lato that is characterized by white carpophores and short spores, only few species have been studied anatomically enough to be sure about the structure of the hymenophoral trama. Those species with completely irregular trama are likely to be *Pleurocybellae*.

Practical importance : Hardly any.

SPECIES

P. porrigens (Pers. ex Fr.) Sing. (Pleurotus, Gillet); ***P. lignatilis*** (Pers. ex Fr.) Sing. (sensu Kuhner 1926) (Pleurotus, Gillet), and var. ***albovirens*** (Quél.) Sing. (sensu Josserand 1943) (Pleurotus, Quél.).

18. NOTHOPANUS Sing.

Mycologia 36 : 364. 1944

Type species : Agaricus eugrammus Mont.

Characters : Habit of the carpophores pleurotoid (very rarely centrally stipitate); pileus dry, glabrous or with radial fibrils (which may be colored), often pigmentless; cuticle little differentiated; lamellae adnate to decurrent, moderately close to distant, usually white; hymenophoral trama subregular-subintermixed to strongly intermixed, often the majority of the hyphae running towards the edge, and the hyphae subparallel at places at least near the edge and in young specimens, but many hyphae running in other directions, and some of them of rather unequal size and shape though predominantly filamentous, with rather thin to thick walls (1-2 μ); cystidioles and hypha-like hymenial bodies sometimes present but

pseudocystidia, leptocystidia, metuloids, etc. absent, even well differentiated cystidioles neither constant nor conspicuous; basidia normal in all regards; spores white in print, hyaline, ellipsoid, or subglobose, never cylindric, with more or less distinct suprahilar applanation, with thin, nonamyloid wall, smooth; stipe present or absent, rarely central, more often eccentric to lateral, frequently colorless (white); veil none; context usually pigmentless, in young carpophores rather soft fleshy but soon becoming tough because of the hyphal walls which become thicker in mature specimens; they are nonamyloid, non-gelatinized; clamp connections present. On dead and on living wood.

Development of the carpophores: Unknown.

Area: Tropics, and subtropics.

Limits: This genus coincides with what used to be called *Panus* in the Fries-Saccardo scheme but differs amply in the thin carphores with little pigmentation, the non cylindric spores, etc. It was therefore separated as *Nothopanus* (i. e. «false *Panus*»). This genus is much closer to the preceding genus than to any genus of the tribus *Lentineae* where one might expect to find related groups. It differs from the species of *Pleurocybella* in the toughness of the old specimens, potentially fibrillose and pigmented pileus, and more distant lamellae. *Nothopanus* is essentially an adaptation of *Pleurocybella* to the climatic conditions of the tropics.

State of knowledge: Nothopanus consists of several species. Two of these are completely known, the others are just well enough known to be referred to this genus without doubt.

Practical importance: The *Nothopani* are undoubtedly wood destroyers and may even cause some damage to living trees. Considering the large number of hosts affected by *N. eugrammus* in Florida, it may turn out that this species is a pathogenic fungus in plantations (*Persea, Citrus,* etc.), but there are no data on this subject in the literature on plant pathology.

SPECIES

N. eugrammus (Mont.) Sing.; *N. guadelupensis* (Pat.) Sing.; *N. vinosofuscus* (Bres.) Sing.; *N. elasticus* Sing.

KEY TO THE SPECIES

19. ANTHRACOPHYLLUM Ces.

Myc. Borneo, p. 3. 1879.

Type species : A. Beccarianum Ces.

Characters . Pileus laterally attached, rarely with a stipe which, however, is not visible from above in most species when they have reached maturity; cuticle of the pileus little or not differentiated, dry, somewhat rough under the microscope, old specimens usually more or less grooved on the surface of the pileus at least its margin along the interlamellar spaces; lamellae distant, intermixed with lamellulae, with entire edge, deep colored even in fresh specimens, more so in dried material, wedge shaped with acute edge; hymenophoral trama subregular-subirregular, with a distinct axillar trend, but the hyphae either individually or in strands strongly interwoven in all directions, narrower than in the trama of the pileus; spores hyaline, but often colored (the cell sap) from the dissolved pigments in KOH (greenish or cinnamon); mostly broadly cylindric but also ellipsoid or oblong to fusoid, smooth, nonamyloid, thin walled; cystidia none of any kind except for pseudoparaphyses which are scattered on the edge and the sides of the lamellae and often slightly thick-walled; basidia normal in all regards, but the sterigmata (usually 4) sometimes deformed and saccate (inability to discharge the spores?); subhymenium present, dense and ramose; pigments very characteristic in the hymenophore, one, brownish cinnamon to deep mahogany red is extracted by alcohol, and also escapes in preparations with KOH (medium becomes cinnamon or mahogany for a short while after the fragment is immerged); there are also carbonaceous particles, most of them clinging to the walls of the basidia and hyphae, sometimes even the spores; they become blue-green in KOH and the greenish solution resulting from it dyes the whole tissue, especially the subhymenium and the basidia, green; context with fewer carbonaceous pigment bodies, thin, consisting of thick-walled, interwoven, nonamyloid hyphae with numerous clamp connections. Veil none. Mostly on wood.

Development of the carpophores Unknown.

Area : Tropics; in some regions penetrating into the warmer belt of the temperate zones.

Limits : This genus has been confused with *Xerotus* which is the same as *Gloeophyllum* and belongs to the true *Aphyllophorales*, near

Daedalea and *Daedaleopsis, Hexagona,* etc. Among the *Lentineae*, this genus is easily recognized by the dark color and the small number of the lamellae, the peculiar pigmentation, and the grooved margin. Among the other *Tricholomataceae*, it comes close to *Nothopanus* from which it differs in larger, often cylindric spores, in the non-fibrillose surface of the pileus, in the pigmentation, and in tougher consistency. Patouillard combined the two genera in one which he (erroneously) called *Xerotus*. His conception of *Xerotus rawakensis* is nothing else but *Nothopanus guadelupensis* (Pat.) Sing.

The genus *Anthracophyllum* is very ambiguous in its position. It must be treated with the *Clitocybeae*, along with *Nothopanus* with which it certainly shares the habit and certain other characters; yet the spores which are more cylindric or at least oblong in a majority of *Anthracophylla* the author has seen, would rather place it in the *Lentineae*. It keys out in both tribus. Significantly, a similar pigment (green in KOH) has been observed by the author in *Collybia alkalivirens*.

State of knowledge : A rather large number of species has been described, all of them very much alike in dried condition. Lloyd who has studied most of the types arrived at the other extreme, thinking that they were all one species. The truth is, according to the experience of the author who has studied the types of *Xerotus nigrita, X. lateritius, X. viticola, X. discolor, X. Berterii, X. fuliginosus*, most probably somewhere in the middle. A complete monograph of the species should include more dependable data from the fresh specimens, and the development of the carpophores of at least one species. At present, the author recognizes 4 species.

Practical importance : The species of this genus must be considered as wood destroyers. The damage they inflict is probably of little economic consequence.

SPECIES

A. nigrita (Lév.) Kalchbr. (Xerotus, Lév.; A. Beccarianum Ces.; ? Panus melanophyllum Fr.); *A. lateritium* (Berk. & Curt.) Sing. (Xerotus, B. & C.; Plicatura, Murr.; Xerotus fuliginosus Berk & Curt.; Xerotus viticola Berk. & Curt.); *A. discolor* (Mont.) Sing. (Xerotus, Mont.); *A. Berterii* (Mont.) Sing. (Xerotus, Mont.).

KEY TO THE SPECIES

A. Species from the southern hemisphere: Juan Fernandez and Southern Chile.
   B. Spores large: 10-13,7 × 5,2-6,8 µ; pigmentation very abundant under the microscope. Juan Fernandez (west of Chile). *A. Berteroi*
   B. Spores smaller: 7,7-10,5 × 5-6,2 µ; pigmentation scanty. Southern Chile. *A. discolor*

A. Species of the American tropics, Asiatic tropics, and north to U. S. A. (as for African species, cf. *Panus melanophyllus* Fr.)
   C. Mature specimens rarely stipitate; margin subincurved; diameter up to 20 mm, lower surface never cinnabarinous, violet, or purple but rather a deep brick red, finally blackish brown. American species. *A. lateritium*
   C. Mature specimens often stipitate with an eccentric blackish brown, minutely tomentose stipe, mycelial tomentum tawny; margin at first strongly incurved; diameter to 30 mm; lower surface cinnabarinous, then violet, then purple, and finally black. Malayasia north to Hongkong. *A. nigrita*

20. TROGIA Fr.

Genera Hymen., p. 10. 1836.

Type species: Cantharellus aplorutis Mont. [*Trogia buccinalis* (Mont.) Pat.].

Characters: Habit of the carpophores omphalioid-pleurotoid, sometimes more omphalioid, sometimes (more rarely) more pleurotoid, but carpophores always stipitate, distinctly reviving after they have dried out in situ when remoistened by rain or artificially; pigment always present (white forms unknown); cuticle of the pileus little differentiated; hyphae of the cuticular layer at first long filamentous and forming a loose trichodermium (Pl. XVII, 2), later agglutinated and pressed down (repent); lamellae very narrow to moderately narrow, entire, usually forked, arcuate and deeply decurrent; spore print white; spores hyaline, smooth, more or less ellipsoid (not cylindric), nonamyloid, rather small; basidia small, normal in all regards but often 1-3-spored (always at least some 4-spored basidia present in any carpophore); cystidia none; edge of the lamellae homomorphous; hymenophoral trama irregular, subintermixed; subhymenium subcellular, a rather thin layer; context thin, distinctly tough but flexible when fresh; hyphae of the trama with somewhat (not strongly) thickened walls, nonamyloid, with clamp connections; stipe tough, fibrous-leathery, solid or nearly so, rising from a pedestal such as also found in *Microporus* (polyporaceous genus, near *Coriolus* but

with pseudostipe), never with rhizoid fibers at the base. On wood, most frequently on hard old logs and sticks.

Development of the carpophores : Unknown.

Area : Tropics.

Limits : This genus is somewhat intermediate between the *Clitocybeae*, the *Lentineae*, and the *Hemimyceneae*. Among the former it is perhaps closest to the genus *Collybia* from which it differs in the strongly decurrent lamellae. Some tropical species of *Hemimycena* have an external appearance much like that of the *Trogiae* but can easily be distinguished by their cheilocystidia and (or) the structure of their cuticle. Nevertheless, the attachment of the stipe to the substratum is much rather like that occuring in the *Hemimyceneae* than that observed in all *Clitocybeae* excepting the *Trogiae*. Since, however, all other characters are those of the *Clitocybeae*, the author prefers, at present, to insert this genus in the tribus *Clitocybeae* as the last genus of the subtribus with clamp connections.

As for the limits of the genus in regard to *Clitocybe* see that genus.

Fries made the mistake to confuse a common northern fungus, *Plicatura* (*Meruliaceae*) with this tropical genus of agarics, but these fungi are too different to cause any difficulty in delimitation.

Patouillard who was one of the few authors who separated *Trogia* and *Plicatura*, emphasizing the fact that the type belongs in the tropical group, nevertheless confused the genus with *Lentinus* in one case, as also did Murrill and other authors. The hymenophoral trama of the *Trogiae*, however, is not regular and its spores are not cylindric ; the attachment of the stipe to the substratum is not the same in both genera, and the lamellae edge is denticulate or lacerate in most cases in *Lentinus*, but entire in *Trogia*. *Panus* has a less developed, and *Pleurotus* a more strongly developed subhymenium than *Trogia*, and in both these genera the hyphal walls are thicker, at least in many hyphae of the hymenophore, their spores are cylindric and the fruiting bodies are comparatively thicker, whereas in *Trogia* the hyphal walls are equally moderately thick, the spores non-cylindric, the fruiting bodies thin. In *Pleurotus* and in *Panus*, the stipe never arises from a pedestal, and metuloids often occur, whereas in *Trogia* the pedestal is very characteristic, and metuloids are never present.

State of knowledge : A revision of the species shows that there are three species that can be considered as belonging to *Trogia*.

SPECIES

T. cantharelloides (Mont.) Pat.; *T. buccinalis* (Mont.) Pat. (Cantharellus aplorutis Mont.; T. Montagnei Fr.; T. infundibuliformis B. & Br.); *T. violaceogrisea* (Henn.) Pat. [? *T. discopoda* (Pat.) Pat.].

KEY TO THE SPECIES

The species indicated above can be easily determined without a key.

Subtribus Tricholomatinae Sing.

Type genus: *Tricholoma* (Fr.) Quél.

Characters: Those of the tribus; clamp connections absent except in a few species of *Omphalina*, *Armillariella*, and *Tricholoma*.

21. OMPHALINA Quél.

Enchiridion Fung., p. 42. 1886, emend. Sing. *Pap. Mich. Ac.* **32**: 124. 1948.

Type species: *O. umbellifera* (L. ex Fr.) Quél.

Syn.: *Omphalia* (Fr.) Quél., *Jura Vosg.*, p. 99. 1872-73 sensu Sing.[41] 1942), emend. Romagnesi (1942) non Gray.

Characters: Habit of the carpophores distinctly and constantly omphalioid, or omphalioid-pleurotoid (i. e. omphalioid but with eccentric to sublateral stipe); pigment none, or present, often abundant, membranal, often incrusting in fragments, either dull colored (gray to almost black) or bright colored (yellow, green, purple, etc.); pileus more or less hygrophanous, glabrous and naked or with scales near the center, with straight or incurved margin, often umbilicate; cuticle consisting of radially arranged, filamentous hyphae and generally little differentiated; lamellae decurrent, sometimes comparatively thick and distant and thus reminding one of *Camarophyllus* or *Hygrocybe* of the *Hygrophoraceae*; spore print pure white; spores hyaline, smooth or rarely echinate, with thin, or rather thin, nonamyloid walls, short ellipsoid, ellipsoid, ovoid, very broadly cylin-

[41] I cannot understand the statement made by Konrad & Maublanc (1948, p. 332): « Singer ... le » [i. e. the genus *Omphalia*] « supprime radicalement ». I never abandoned *Omphalia* (or *Omphalina*).

dric, or tibia shaped; basidia normal in all regards but frequently 2-spored; cystidia none except for very scattered and inconspicuous cheilocystidia in some species; hymenophoral trama irregular, rarely regular and then very narrow and partly replaced by a very irregular subhymenium (the species with a regular narrow trama have orange pigment that dissolves in ammonia), the hyphae of the irregular trama opaque and somewhat thick walled, nonamyloid; stipe fleshy to subcartilaginous, narrowly hollow or stuffed becoming hollow, 1-2, rarely more millimeters thick; central or eccentric to sublateral in a few species; rhizomorphs none (at least no black rhizomorphs observed); context often hygrophanous, watery, thin, consisting of partly thick walled hyphae with or without clamp connections. On rocky soil, on sand, on dead wood, on buried wood, among (or on) moss.

Development of the carpophores: Unknown.

Area: With certainty only in the temperate and cold zones.

Limits: The delimitation of this genus against *Clitocybe* has been discussed in that genus. *Omphalina* is much closer to *Armillariella* than to *Clitocybe*. The two genera can be distinguished by their size, in most cases, and the smallest species of *Armillariella* (*A. Saviczii*) differs from all species of *Omphalina* by the presence of rhizomorphs and a veil. *Armillariella chrysophylla* is also reminiscent of *Omphalina*, not so much because of its size but because of its omphalioid habit (the stipe is only 2-5 mm thick and soon becomes hollow), but it can be distinguished from all *Omphalinae* by its yellowish spore print, and from all *Omphalinae* that lack clamp connections, by its larger size and strongly incurved margin of the pileus. As far as *A. chrysophylla* is concerned (and perhaps a few species that seem to be closely related to it), its inclusion in *Omphalina* might be just as good a solution as the insertion in *Armillariella* as proposed by the author. However, in this case the diagnosis of *Omphalina* would have to be emended in order to include species with colored spore print. If it should turn out later that the group *Armillariella chrysophylla* also includes species with white spore print, or that *Omphalina* in our present delimitation also contains species with yellow spore print, it may perhaps become preferable to revise the limits between the two genera in regard to *A. chrysophylla*. At present, the author believes that the delimitation is satisfactory, and *Armillariella* and *Omphalina* are considered as two closely related but distinguishable genera.

Trogia and *Nothopanus* have constantly clamped hyphae and reviving carpophores whereas *Omphalina* has often clampless hyphae and non reviving carpophores.

Lepista and *Rhodocybe* are usually larger than the species of *Omphalina* and will not be confused with the latter genus. Moreover, the spores of these genera are rough (not echinate) and pinkish in print.

Resupinatus often has a hymenophoral trama reminiscent of *Omphalina* subgenus *Romagnesia* but the pigmentation of the former is too different from that of the latter to cause any doubt in determination. Moreover, the trama in *Resupinatus* is partly gelatinized which is not the case in *Omphalina*.

The species of *Marasmiellus* that have decurrent lamellae have formerly been confused with *Omphalina*, and even some species of *Mycena* have been included in *Omphalina*. One species of *Xeromphalina*, several of *Hydropus*, one of *Cantharellula*, and several of *Fayodia* were also currently considered as *Omphalina* by the Friesian school in taxonomy. All these species differ clearly from *Omphalina* in having amyloid spores or diverticulate epicuticular hyphae, and usually very distinct cheilocystidia and or cystidia. They do not key out here in the keys provided in this book, and in the author's opinion, are not very closely related to *Omphalina* proper.

As for the delimitation from *Leptotus*, see that genus.

State of knowledge: The knowledge of the species of *Omphalina* has recently been emended by a few short papers by Romagnesi, Kühner, Josserand and this author. The genus has been monographed by Kavina; however, few of his descriptions contain enough vital information to be of use in the necessary rearrangement of the species. Consequently, a monograph of *Omphalina* would be very desirable at this moment. The author has studied a number of type specimens, yet, many species are now without type specimens, and their interpretation rests with the judgment of the taxonomists interested in them who, naturally, differ in several cases. Therefore, some binomials are supplemented with « sensu N » wherever precision is wanted. The uncertainty that is prevalent in so many specific cases is often felt by the taxonomist who attempts to straighten out the classification of the genus, or its delimitation. For instance, *O. Alleni* Maire, described from England, has not recently been studied, yet, it is possible that this species would be important in any question that concerns the delimitation of *Omphalina* against

Armillariella. The author admits at present 11 species in this genus.

Practical importance : None.

SPECIES

Subgenus I. **Eu-Omphalina** Sing. (1948) (genus *Omphalia* sensu Kühner). Trama wholly irregular; pigment never orange, and never dissolving lemon yellow in ammonia. Type same as in genus.

Sect. 1. FIBULATAE Romagnesi (1942). Hyphae of the carpophore with clamp connections except in parthenogenetic forms.

Type species : O. demissa (Fr. sensu Romagnesi) Quel.

O. demissa (Fr. sensu Romagnesi) Quél.; *O. griseopallida* (Desm.) Quél.; *O. Gerardiana* (Peck) Sing. (Clitocybe, Sacc.); *O. epichysium* (Pers. ex Fr.) Quél.

Sect. 2. GENUINAE Romagnesi (1942). Hyphae of the carpophore without clamp connections in homothallic and heterothallic forms.

Type species : O. umbellifera (L. ex Fr. sensu Romagnesi) Quél.

O. philonotis (Lasch) Quél. [Omphalia sphagnicola (Berk. apud W. G. Smith) Karst.; Omphalia telmatiaea (Berk. & Cooke) Sacc.]; *O. oreades* Sing.; *O. umbellifera* (L. ex Fr. sensu Romagnesi) Quél.; *O. abiegna* (Berk. & Br.) Sing. (Agaricus umbelliferus var. abiegnus Bk. & Br.); *O. olivaria* (Peck) Sing. (Agaricus, Peck; Omphalia, Sacc.; Omphalopsis, Murr.; ? Agaricus infumatus B. & Br.); probably also *O. chlorocyanea* (Pat.) Sing. [Agaricus, Pat.; Omphalia viridis (Fl. D. ex Quél.) Lange].

Note : O. abiegna is perhaps not specifically different from *O. olivaria*.

Subgenus II. **Romagnesia** Sing. (1947). Pigment orange in fresh carpophores, dissolving in ammonia to a lemon yellow solution, probably intercellular; a narrow regular hymenophoral trama usually present but flanked by an irregular very broad subhymenium.

Type species : O. Postii (Fr.) Sing. (sensu A. H. Smith).

Species with clamp connections :

O. brevibasidiata (Sing.) Sing. (Clitocybe, Sing.).

Species without clamp connections :

O. Postii (Fr. sensu A. H. Smith) Sing. [Omphalia, Karst. sensu A. H. Smith; ? Omphalia fibuloides (Peck) Sacc.]

Subgenus III. **Omphaliopsis** (Pilát in Kavina & Pilát, *Atlas* ...

rand (1944). Pigment none: hymenophoral trama as in subgenus II; habit most frequently distinctly pleurotoid.

Type species: Pleurotus mutilus (Fr.) Gillet sensu Josserand Pilát p. p.?

O. Josserandii Sing. [Pleurotus mutilus (Fr.) Gillet sensu Josserand].

Note: The author has not studied the species described by Josserand but it is evidently different from *Clitopilus scyphoides* var. *typicus* f. *mutilus* (Fr.) Sing. which in the author's opinion is the true Friesian *Agaricus mutilus*. Pilát's description has characters of both Fries' and Josserand's *P. mutilus*, but his reference to Bresadola's *P. fimbriatus* var. *mutilus* and the description of the spores make it more problable that it is at least predominantly the same as Josserand's fungus. Josserand's precise description makes the insertion of this species in *Omphalina* a necessity. Josserand himself cites Pilát's section as the proper subdivision where his fungus belongs; consequently, the author felt that it is safe to follow Josserand in his disposal of *Pleurotus mutilus* sensu Josserand with the modifications due to the classification used in the present treatment. The correctness of the insertion of *O. Josserandii* in a special section *Omphaliopsis* of *Omphalina* depends on the correctness of Josserand's data.

KEY TO THE SPECIES

A. Clamp connections present

B. Pileus bright yellow; stipe white, then yellow; in *Sphagnum* in Asia. — *O. brevibasidiata*

B. Pileus not bright yellow, but either some kind of purple, or dull colored (if carpophore white and pleurotoid, see subgenus *Omphaliopsis*; otherwise: « C »).

C. Lamellae purple; pileus purplish at first. — *O. demissa* [45]

C. Lamellae not purple; pileus not purplish at first.

D. Sphagnophilous species of medium size. — *O. Gerardiana*

D. Not or coincidentally in *Sphagnum*; carpophores usually small.

E. On trunks; Europe. — *O. epichysium*

E. On the ground.

F. Spores 8.2-10.5 × 5-6.8 μ, basidia bisporous; typical, 2-spored form of — *O. griseopallida*

F. Spores slightly narrower; basidia tetrasporous. Rarer 4-spored form of — *O. griseopallida* (probably *O. rustica* sensu Rea)

[45] Cf. *Clitocybe hyacinthina* Sing., *Ann. Myc.* 41: 46, 1943, which may also be an *Omphalina* rather than a *Clitocybe*. It differs from *O. demissa* in spore size.

A. Clamp connections absent.

G. Pileus bright orange; moist places among moss; strand of the hymenophoral trama consisting of more or less thin-walled and parallel hyphae; pigment dissolving in ammonia into a lemon yellow solution. *O. Postii*

G. Not combining these characters.

H. Pileus brown to gray or almost black; not on fir wood.

I. Sphagnophilous species of medium size. Europe. *O. philonotis*

I. Not or coincidentally in *Sphagnum*.

J. Spores 6-8-8,2 × 3-3,7 μ. Alpine zone of the White Mts in North America. *O. oreades*

J. Spores 4 μ or broader. Area unknown, described from Europe. *O. umbellifera*

H. Pileus some other color; on fir wood.

K. Disc of the pileus olive, margin yellowish green; lamellae light yellow to lemon yellow. North America and Pyrenées, perhaps also in England. *O. olivaria*

K. Disc yellow, the whole pileus bleaching, pallid forms also frequent; lamellae whitish cream color to light yellow. Montane and subalpine zone of the mountain ranges of the northern hemisphere. *O. abiegna*

22. ARMILLARIELLA Karst.

Hymenomycetes Fennici, *Acta flor. faun. Fenn.* **2**: 1 . 4. 1881 em. Singer 1942, 1943, em.

Type species: *A. mellea* (Vahl in *Fl. Dan.* ex Fr.) Karst.

Syn.: *Aeruginospora* Hoehnel, *Sitz.-ber. k. Akad. Wiss. Wien, math.-nat.-wiss. Kl.* **117**: 1012. 1908.

Characters. Habit of the carpophores clitocyboid, sometimes somewhat reminiscent of *Camarophyllus*; pigment either intercellular (or membranal), or intracellular, yellow, brownish melleous, umber, blackish fuscous, etc. Pileus squamulose, or fibrillose, or punctate, or lineate, or smooth and glabrous, hygrophanous or non-hygrophanous, non-viscid; cuticle often little differentiated, and often somewhat differentiated, e. gr. with a fragmentary hymeniform epicutis; lamellae close to distant, moderately thick to rather thick, adnate to more often decurrent; hymenophoral trama regular, or almost irregular at times; spore print somewhat colored, usually pale ochraceous, more rarely white; spores often with moderately thick wall; hyaline, short ellipsoid, ellipsoid oblong, subglobose, etc., nonamyloid; basidia completely normal, usually 4-spored but sometimes 2-spored, at times some sclerotized basidia without spore formation observed, in occasional forms the basal septum of the

basidium clamped even though all the other hyphae of the carpophore may be clampless; in some species the basidia may be somewhat longer than normal; cheilocystidia frequently present; cystidia usually none on the sides of the lamellae; stipe fibrous-fleshy or fleshy, eventually often becoming somewhat hollow (but not cartilaginous or thin, fragile, and tubulose), (2) 4 mm broad or broader; rhizomorphs often present; veil sometimes present, annulate, but in the majority of the species it is absent; context fleshy, not tough, not reviving, often with disagreeable taste; hyphae thin walled to moderately thick-walled; without clamp connections, or rarely with scattered, inconstant clamp connections, nonamyloid. On wood, among deep moss, more rarely on earth.

Development of the carpophore : Hemiangiocarpous in *A. mellea :* unknown in the evelate forms (except for *A. chrysophylla* which is gymnocarpous according to Blizzard but the determination of the specimens studied remains to be verified).

Area : Probably cosmopolitan, or almost so.

Limits : Some of the species admitted here, were formerly considered as belonging to *Armillaria, Lepiota, Clitocybe,* or *Hygrophorus (Camarophyllus). Armillaria* is now restricted to *A. luteovirens* and allied species which differ from *Armillariella* in bilateral trama, and amyloid spores, the presence of clamp connections, and sinuate adnexed to subfree lamellae. It is therefore not even related with *Armillariella.* The other species of *Armillaria,* now not considered as belonging in that genus, were mostly transferred to *Tricholoma* (these species differ from *Armillariella* in white spore print, distinctly sinuate emarginate lamellae, and always very thin walled spores). *Armillariella mellea* has been considered as a species of *Lepiota* by Lange but aside from the fact that very old spores are occasionally very slightly pseudo-amyloid in this species, there is no other basis for this transfer.

This leaves mainly two genera viz. *Clitocybe* and *Camarophyllus.* In the author's opinion, both these genera are sufficiently different from *Armillariella* because of the presence of clamp connections in both of them. Besides, the hymenophoral trama in *Armillariella* consists of hyphae that are somewhat thicker in an average, and more axillarly arranged in young specimens than they are in *Camarophyllus.* The species formerly considered as *Hygrophoraceae* (i. e. *A. hymenocephala,* etc.) might also be inserted in *Omphalina* rather than *Armillariella.* However, unless the delimitation between the

genera *Armillariella* and *Omphalina* is changed in the future on the basis of additional data (see paragraph on limits in *Omphalina*), *A. hymenocephala* and allied species will be considered as *Armillariella* rather than *Omphalina*, according to the delimitation adopted in the present book.

State of knowledge : Seventeen species are completely known; a few more may be added later. These species are not difficult to recognize as *Armillariellae* if the macroscopical characters are not overemphasized, and they are also not difficult to separate from each other.

Practical importance : A. mellea and *A. tabescens* are of great importance as destroyers of trees in forests and plantations, in parks, along alleys and in gardens. They damage even such crops as peanuts and sweet potatoes. *A. mellea* is considered as a good edible mushroom in many countries, especially in eastern Europe. For more detailed data on the host range and the specific damage as well as methods of control, the reader is referred to the phytopathological literature where the fungi concerned are, to this very day, called *Agaricus melleus* or *Clitocybe mellea*, or *Armillaria mellea*, and *Clitocybe tabescens*, or *C. monadelphus* respectively. Both these plants can usually be recognized by their black rhizomorphs.

SPECIES

No sections have as yet been proposed for these species. In future, it may be well to distinguish a section of genuine Armillariellas from the section *Microspora* Sm. & Hesl. (in sect. *Hygrophori*), but a clear delimitation of these sections (possibly under addition of a third section) will be achieved only after a monographic study. Consequently, we do not segregate the species in groups.

A. mellea (Vahl in *Fl. Dan.* ex Fr.) Karst.; *A. Sariezii* Sing.; *A. Puiggarii* (Speg.) Sing.; *A. tabescens* (Scop. ex Fr.) Sing. (Clitocybe, Bres.); *A. ectypa* (Fr.) Sing. (Omphalia, Quel.); *A. Watsonii* (Murr.) Sing. (Monadelphus, Murr.); *A. nigropunctata* (Secr.) Sing. (Clitocybe, Gillet); *A. chrysophylla* (Fr.) Sing. (Omphalia, Gillet); *A. compressipes* (Murr.) Sing. (Clitocybe, Murr.); *A. alachuana* (Murr.) Sing. (Clitocybe, Murr.), *A. Azalearum* (Murr.) Sing. (Clitocybe, Murr.); *A. singularis* (Hoehnel) Sing. (Aeruginospora, Hoehnel); *A. paupertina* (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.); *A. deceptiva* (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.); *A. microspora* (Sm.

& Hesl.) Sing. (Hygrophorus, Sm. & Hesl.); *A. hymenocephala* (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.); *A. ditopa* Sing.; perhaps also *Omphalia atropuncta* (Pers. ex Fr.) Sacc. (Omphalina, Quél.; Eccilia, Gillet) which is said to be close to *A. hymenocephala*; and *Armillaria fuscipes* Petch which is said to be close to *A. mellea*.

KEY TO THE SPECIES

A. Veil present, annulate; rhizomorphs black, abundant.

B. Taste astringent.

B_1. Pileus 30 mm in diameter or broader; rhizomorphs 250 μ thick or more. — *A. mellea*

B_1. Pileus 7-10 mm broad; rhizomorphs 100-200 μ thick. In White Russia. — *A. Saviczii*

B. Taste mild. — *A. Puiggarii*

A. Veil none.

C. Spores 8,5-12,5 × 4,8-5,8 μ, i. e. at least a certain percentage of the spores rather elongate; pileus deeply umbilicate; lamellae usually bright yellow; growing on wood. — *A. chrysophylla*

C. Spores globose or ellipsoid, mostly rather short; pileus not deeply umbilicate (but often depressed); lamellae not bright yellow; growing on wood or on some other substratum.

D. Growing caespitosely; pileus non hygrophanous; pigment incrusting; habit of the carpophores as in *A. mellea* (but without annulus). — *A. tabescens*

D. Not combining these characters.

E. European and Asiatic species.

F. Pileus white with blackish points or lines. — *A. nigropunctata*

F. Not so (compare *Omphalia atropuncta*, if cuticle is differentiated).

G. Pileus grayish brown, the center often rufescent; growing under bamboo; spores said to be greenish. Tropical Asia. — *A. singularis*

G. Pileus gilvous-ochraceous or melleous with brownish fibrils; growing among moss or *Carex*; spores cream color in mass; temperate-boreal species. — *A. ectypa*

E. American species.

H. Pileus uniformly pale fulvous, strongly innately fibrillose-subvenose, nonhygrophanous; spores 7,2-8,2 × 4,5-5,5 μ; lamellae decidedly decurrent. Florida. — *A. Watsonii*

H. Spores up to 7,8 μ long in some species, or smaller, not combining the above characters.

I. Context very bitter. Florida. — *A. alachuana*

I. Context perfectly mild to acidulous.

J. Spores 5-7,8 × 5,2-6,7 μ; odor striking, disagreeable; lamellae very narrow. California. — *A. pauperlina*

J. Spores smaller (either shorter, or narrower); odor slight and earthy, or none; lamellae not exceedingly narrow. Eastern and Southern species.

K. Pileus 40-80 mm broad; spores 6-7,5 × 4,5-5,5 μ; color of the surface of the pileus dark umber brown; lamellae close; context gray or watery brown; fruiting in winter in Alabama *A. compressipes*

K. Pileus smaller; spores smaller; or else color of the pileus not dark umber brown and the lamellae not close, and not fruiting in winter

L. Arthrospores present on stipe. Argentina *A. ditopa*, ined.

L. Arthrospores none. North American species.

M. Spores 3,5 μ broad or less; lamellae narrow. Michigan. *A. microspora*

M. Spores often broader than 4 μ, or else lamellae broad.

N. Lamellae narrow; pileus 45 mm broad; spores 6-7 × 3,7-4,7 μ; fruiting in summer in Florida. *A. Azalearum*

N. Lamellae broad; pileus smaller; spores smaller; fruiting in summer in North Carolina and Tennessee.

O. Epicutis almost hymeniform at places; lamellae distant to subdistant (15-20 through-lamellae). *A. hymenocephala*

O. Epicutis not at all hymeniform; lamellae subdistant to close (26-32 through-lamellae) *A. deceptiva*

23. TRICHOLOMA (Fr.) Quél.

Champ. Jura Vosges, p. 76. 1872-73, non Benth. (1820).

Type species: *Tricholoma equestre* (L. ex Fr.) Quél. [= *Tricholoma flavovirens* (Pers. ex Fr.) Lundell].

Syn. *Cortinellus* Roze, *Bull. Soc. Bot. Fr.* **23**: 51. 1876.
Gyrophila Quél., *Enchir.*, p. 9. 1886.
Mastoleucomyces Batt. ex Kunze, *Rev. Gen. Pl.* **2**: 860. 1891.
Glutinaster Earle, *Bull. New York Bot. Gard.* **5**: 433. 1909.
Monomyces Batt. ex Earle, *Bull. N. Y. Bot. Gard.* **5**: 442. 1909.
Sphaerocephalus Batt. ex Earle, *Bull. N. Y. Bot. Gard.* **5**: 447. 1909.
? *Nemecomyces* Pilát, *Ann. Mycol.* **31**: 51. 1933.

Characters : Habit of the carpophores tricholomatoid; pileus viscid, or non viscid, glabrous or innately to tomentosely fibrillose, naked to squamose or even squarrose, never hygrophanous, with the pigment — where present — incrusting the hyphal walls in most of the clampless species, otherwise all dissolved in the cell sap; cuticle consisting of interwoven, little differentiated hyphae, or of rather subparallel, thin hyphae, or of strictly parallel broad hyphae (and then hyphae practically always without clamp connections), or (rather rarely) with hymeniform epicutis (and then hyphae also clampless); lamellae usually very distinctly emarginate sinuate, always strongly so in the clamp-bearing species, sometimes more adnexed or almost adnate in the clampless species, never decurrent, thin to medium thick (in some clampless species), subhorizontal, rarely subascendant at first; spore print pure white, rarely pale cream color, never truly cream pink or pink, never greenish; spores hyaline, usually with very thin smooth wall, nonamyloid, very rarely a few old spores somewhat pseudoamyloid, ellipsoid to subglobose, more rarely fusoid, cross shaped, or subangular, with or without suprahilar depression or applanation; basidia normal in all regards, 4 spored, very rarely 2 spored; cystidia usually none, rarely present in the form of cheilocystidia, more rarely some cystidia present on the sides of the lamellae but then never of the *Inocybe* or the *Melanoleuca* type, all kinds of cystidia constantly absent in the species provided with clamp connections; hymenophoral trama regular to almost subregular, with thin parallel to somewhat interwoven rather thin, elongated hyphae; stipe central, fleshy to fleshy fibrillose, sometimes very hard but never cartilaginous or leathery or horny in any species known, solid, stuffed, or hollow, never tubulose, veil absent, or somewhat cortina-like, or consisting of a fleshy annulus, or an annular zone at the apex of the stipe, more rarely membranous; context of the pileus fleshy, mild, acrid, or bitter, often strongly reacting with one or several of the usual reagents (formaline phenol, KOH, methylparamidophenol, acids, etc.); hyphae ordinarily thin walled, elongated, nonamyloid, with or without clamp connections (rarely clamps absent except between the subhymenial hyphae and the basidium). Mostly on earth in the woods, more rarely in open fields, or prairies and semideserts, very rarely on wood or in deep moss (and then hyphae without clamp connections).

Development of the carpophores : Unknown but in some species at least pseudoangiocarpous.

Area. Mostly in the temperate and subtropical zones, very few species reaching the tropics.

Limits: The clampless species can be distinguished from the other fleshy genera of the *Clitocybeae* by the lack of clamp-connections and the attachment of the lamellae, the latter character distinguishing the Tricholomas from *Armillariella*. The species with incrusting pigment are considered as belonging in the subgenus *Globulicutis* of *Tricholoma* even though the lamellae may not be strictly emarginate-sinuate, and, on the other hand, the species with intracellular pigment are considered as belonging to *Armillariella* if the clamp connections are lacking, even though the lamellae may not be strictly decurrent.

The delimitation of the clamp-bearing groups is somewhat more difficult. We consider as Tricholomas only those clamp-bearing *Clitocybeae* which have distinctly emarginate-sinuate lamellae, white spore print, and habitat on the soil; these species have no cheilocystidia. In this manner, it is not difficult to eliminate such species of *Collybia* as *C. maculata* and allied forms as well as the species of *Tricholomopsis*, *Lepista*, *Hypsizygus*, *Laccaria*, etc. In fact, all the species that make it impossible to use the old Friesian delimitation between *Clitocybe* and *Tricholoma* can easily be eliminated since they form natural groups outside *Tricholoma* as well as *Clitocybe*, and the two genera, *Clitocybe* and *Tricholoma*, in the narrowest sense appear to be well distinguishable on the basis of the Friesian diagnostic characters.

There is no doubt that the genus *Tricholoma* as accepted here (and also by all other authors at present) combines a wide variety of forms ranging from species which are anatomically almost identical with *Clitocybe*, to species differing from the latter genus in almost all important anatomical characters. It is certainly tempting for those mycologists who give more emphasis to microscopical characters than to the external appearance, to attempt a separation of the clamp-bearing group of *Tricholoma* from the clampless group, or of the species with intracellular pigment from those with intercellular or membranal pigment. The species with clamp connections or with intracellular pigment would then be combined with the genus *Clitocybe* and the rest would represent the genus *Tricholoma* sensu strictissimo. The author believes that this strictly anatomical-cytological solution is impractical because of the absence of sharp lines between the clamp-bearing and the clampless species as well as between the species with intracellular and those with intercellular or membranal

pigment. In the subgenus *Sericeiculis*, section *Sericella*, there are several species in which the number of clamp connections is low — but variable, and in the same form we sometimes find a few clamp connections while in other specimens none at all are observed. This is especially true for *T. album*, *T. sulphurescens*, etc. As for the pigment, the absence of coloring matter in many species makes it theoretically and practically impossible to draw a sharp line between the groups based on the topography of the pigments. Consequently, it becomes obvious that the difficulties arising from an anatomical-cytological classification of the *Clitocybe-Tricholoma* complex would be even greater than the difficulties arising from a macro-morphological classification. It appears to the author that the genus *Tricholoma* in its present limits is a large genus with, consequently, a wide variety of characters, but not by any means an artificial unit.

In the present delimitation, *Tricholoma* contains all the original species of *Cortinellus*, most tricholomatoid (in habit) species of *Armillaria* except for the type of that genus, *A. luteovirens*; it also contains the bright colored clampless species of *Hygrophorus* (the dull colored ones are mostly *Armillariella*), mainly *Tricholoma marginatum* (*Hygrophorus marginatus*). This species has a more elongated stipe than Tricholomas usually have, and the lamellae are not in all specimens distinctly emarginate-sinuate; yet the bright colors, the absence of clamp connections, its affinities, and its chemical characters are definitely in favor of insertion in the genus *Tricholoma* rather than *Hygrophorus* (or rather *Hygrocybe*) where it has been placed by Peck and others merely on the basis of the bright colored pigment reminiscent of some *Hygrocybe*. But even the pigment is by no means identical in its chemical characters with similar pigments in *Hygrocybe*, nor does it exactly match any of the colors occurring in that genus.

The author has followed Kühner in dividing the species with tricholomatoid habit and hymeniform epicutis (or with epithelium) in a group with close affinities to *Tricholoma* (the species without clamp connections, with « normal », i. e. not granular, basidia in aceto-carmine and with incrusting pigment and a group with very different affinities that has clamp connections, granular basidia in aceto-carmine and intracellular pigment. The latter group is very close to the group of *Tricholoma cerinum* which has been separated by Kühner under the generic name of *Calocybe*. The author thinks that the genus *Calocybe* is a very natural genus that is not closely related to *Tricholoma*.

It has been reported that *T. irinum* has pale pinkish spore print. It seems that a confusion of species has taken place here. There is also a white spored (on white paper) species that is often determined as *T. irinum*, and this has smooth spores in all media under oil immersion lens. It belongs to *Tricholoma*. The other species, with pale pinkish spore print, has slightly roughened spores, and belongs in *Lepista*. There is no doubt but that *Lepista* and the subgenus *Contextocutis* are closely related but the separation on the basis of spore color and spore ornamentation still holds. The hiatus between the two groups involved is distinct enough as long as it is based on this double character.

State of knowledge: The European species of the genus *Tricholoma* were once considered as the best known group of agarics. In spite of a large amount of taxonomic work devoted to the genus *Tricholoma* since the days this opinion was published, it cannot be said that it still holds true. Several groups of species are extremely difficult and in need of monographic treatment, e. g. *T. terreum* and allied species, *T. flavovirens* and allied species, *T. imbricatum* and allied species, *T. pessundatum* and allied species, *T. atrosquamosum* and allied species. The more extensive use of chemical reactions will probably help in segregating larger groups within the present sections. The insertion of the American, South African, Australian, and other non-European species in the scheme of subdivisions is far from complete. It would be desirable to extend the type studies on American material at least so far as to obtain the necessary microscopical data on all of them in order to be able to dispose of them in the natural classification of the genus *Tricholoma*. The classification itself appears to be sound since none of the numerous type studies on American material has essentially altered the principles on which it was founded. But the number of species that at present can be inserted is very small when compared with the number of species described. The author admits 79 species in *Tricholoma*, but the number that will appear in a future monograph will presumably be much higher.

Practical importance: Some species are important edible mushrooms (*T. flavovirens*, *T. sulero*, *T. flavobrunneum*, *T. portentosum* in Europe; *T. mongolicum*, *T. matsutake* in Asia, and *T. Murrillianum* in North America). *T. matsutake* is economically the most important species of all since it is collected in enormous quantities in Japan, and sold in the markets in fresh as well as in dried condition and in cans. But for every good edible *Tricholoma*, there is a poisonous one

(e. gr. *T. stans*, *T. pardinum*, *T. atrosquamosum*, and perhaps forms of the *sulphureum*- and the *virgatum* group). Anybody who wants to exploit the edible species in this genus has to become an expert in distinguishing them from the non-edible species and those with unknown qualities. Among the potentially important species, one may name all the mycorrhizal species and a number of species (such as *T. saponaceum*) that have been shown to have antibiotic properties. Among the former (mycorrhizal) species, some are specific for conifers, or for *Pinus* in particular (*T. flavovirens*, *T. pessundatum*, *T. flavobrunneum*, etc.), or for *Larix* in particular (*T. psammopodum*), and some are specific for frondose trees, etc. A few species do not seem to form mycorrhiza at all, especially some species in the subgenus *Contextocutis*.

SPECIES

Subgenus I. **Contextocutis** Sing. (1945) (= sect. *Contextocutis* Sing. 1943, p. p.). All hyphae with clamp connections; cuticle of strongly and thoroughly interwoven hyphae, little differentiated (denser); pigment exclusively intracellular or absent; mycelium forming mycorrhiza or developing independent of mycorrhiza.

Type species: *T. saponaceum* (Fr.) Quel.

Sect. 1. **LEUCORIGIDA** Sing. (1945). Pileus, lamellae, and stipe white; spores ellipsoid; mycelium growing independent of forest trees, often in fields, meadows, prairies, steppes, semideserts, etc.

Type species: *T. mongolicum*.

T. mongolicum Imai; *T. altaicum* Sing.; *T. farinaceum* (Murr.) Murr.

Sect. 2. **RIGIDA** (Fr. em.) Sing. (1945). Pigmented species, sometimes characteristically discoloring with strong acids; spores ellipsoid, or almost subglobose, or fusoid, pure white in print; mycelium sometimes growing independently of forest trees (?) but mostly forming some kind of mycorrhiza, or at least having some symbiotic or epibiontic relation with trees.

Type species: *T. saponaceum* (Fr.) Quel.

T. irinum (Fr.) Quel. (Rhodopaxillus, Kühner); *T. boreale* (Fr.) Karst.; *T. sudum* (Fr.) Quel. sensu Lange [? = T. sublutidum (Murr.) Murr. = T. Watsonii (Murr.) Murr.]; *T. saponaceum* (Fr.) Quél. [? = T. oliveum Burt; ? = T. ferruginascens (Murr.) Murr.]; *T. viridilutescens* (Peck) Sacc.; *T. huronense* A. H. Smith.

Sect. 3. **IORIGIDA** Sing. (1945). Pileus, stipe, or lamellae, or all of them, with a purplish, or violet, or lilac vinaceous tint; spores pure white or pale cream color (not pink) in print, with very thin walls, cross-shaped or subangular. Biologically similar to the species of sect. 2.

Type species : T. pseudosordidum Sing.

T. pseudosordidum Sing. ; *T. goniospermum* Bres. ; *T. prophyrophyllum* Imai ; *T. Cossonianum* Maire.

Sect. 4. **OCCIDENTALIA** Sing. (1948). Pileus, lamellae and stipe neither all pigment less nor with purple, violet, or lilac-vinaceous tints ; spores subfusiform. Carpophores rising from a characteristic fleshy mass comparable to the carpophoroids of *Rhodophyllus abortivus.*

T. sclerotoideum Morse.

Note : This section as well as the species close to it but arising directly from the soil, e. gr. *Tricholoma fusisporum* Sing. (T. fumosifolium A. H. Sm. & Hesl.) are very close to *Clitocybe inornata* and should perhaps be transferred to that genus.

Subgenus II. **Humidicutis** Sing. (1948). Clamp connections never present ; pigment not incrusting and very bright orange to light orange in the lamellae ; cuticle a cutis consisting of parallel hyphae of small diameter ; pileus sometimes subhygrophanous, often transparently striate when moist, glabrous or fibrillose, not squamose, not distinctly viscid ; odor mephitic, or none ; lamellae rather thick and not crowded ; mycorrhizal relationship unknown.

Type species : T. marginatum (Peck) Sing.

Sect. 5. **MARGINATA** Sing. (1948). Characters of the subgenus ; type of the subgenus.

T. cxnicum (Sing.) Sing (Hygrocybe, Sing.) ; *T. marginatum* (Peck) Sing. (Hygrophorus, Peck) with var. *olivaceum* (Sm. & Hesl.) Sing. (Hygrophorus, Sm. & Hesl.) ; *T. auratocephalum* (Ellis, Sing. (Hygrophorus, Ellis).

Subgenus III. **Sericeicutis** Sing. [= sect. *Sericella* (Fr.) Quel. sensu lato]. Hyphae either all without clamp connections, or some clamps present either on the base of the basidia, or scattered in the carpophore or in the covering of the stipe ; if clamps are found at all, the carpophores are little pigmented (yet growing in the woods, and pileus not viscid) and have a strong characteristic odor of the flowers of *Philadelphus* or *Inocybe corydalina,* or of hemp, or of lighting gas ; cuticle consisting of interwoven to subinterwoven subparallel hyphae (oc-

casional strands of parallel hyphae); pileus, at least its marginal portion, consequently macroscopically sericeous; mycelium of some species known to form mycorrhiza.

Type species : *T. sulphureum* (Bull. ex Fr.) Quél.

Sect. 6. **SERICELLA** (Fr.) Quél. (1872-73) sensu str. (*Sulphurea* Konr. & Maubl. 1924-37). Clamp connections sometimes present; odor striking; lamellae close to distant. Type species as in the subgenus.

T. album (Schaeff. ex Fr.) Quél.; *T. sulphurescens* Bres.; *T. stiparophyllum* Lund; *T. lascivum* (Fr.) Quél. sensu Lange; *T. inamoenum* (Fr.) Quél.; *T. platyphyllum* (Murr.) Murr.; *T. sulphureum* (Bull. ex Fr.) Quél.; *T. chrysenteroides* (Peck) Sacc. [T. malodorum (Murr.) Murr.]; *T. bufonium* (Pers. ex Fr.) Gillet; *T. odorum* Peck; *T. rhodophyllum* (Metrod) Sing.

Sect. 7. **POLYPHYLLINA** Sing. (1943, ut subsectio). Clamp connections constantly absent; odor none; lamellae subclose to crowded; mostly pigmentless or almost so, not viscid.

Type species : *T. columbetta* (Fr.) Quél.

T. columbetta (Fr.) Quél.; *T. virgineum* (Murr.) Murr.; possibly also a small colored species: *T. adustum* (Murr.) Murr.

Subgenus IV. **Fibulicutis** Sing. (1948). Clamp connections present and numerous; pigment not incrusting or not strikingly so; cuticle consisting of parallel hyphae which are strictly repent in the center of the pileus and have a small diameter (2-6 µ); macroscopically innately fibrillose and hirsute on the young margin (at least in the type species), never viscid; odor slight or none; lamellae moderately thick, crowded; mycorrhizal relationship unknown but symbiosis with forest trees probable.

Sect. 8. **GLAUCOALBA** Sing. (1948). Characters of the subsection, and same type:

T. glaucoalbum Sing.

Note : This subgenus differs from *Eu-Tricholoma* in narrow cuticular hyphae in spite of non viscid pileus, and the presence of clamp connections.

Subgenus V. **Eu-Tricholoma** Lange (1933) em. Sing. (1943). (*Armillaria* subgenus *Verarmillaria* Imai 1938). Clamp connections never (or very exceptionally)[a] present; pigment usually distinctly incrusting the hyphal walls (if present); cuticle a cutis as in the preceding

[a] Occasional clamps are observed in the lower surface of the stipe in certain species since in these the mycelium is clamped while in others it is clampless.

section but the parallel hyphae of which it consists rather broad if the pileus is dry, and narrower if the pileus is viscid, macroscopically, the pileus is dry (and then cuticular hyphae 7 μ or more in diameter), or viscid (and then hyphae usually 2-4-6 μ in diameter), in the latter case either glabrous or not glabrous, if dry, rarely subglabrous, usually either tomentose, or tomentose-scaly, or squamulose, squamose, squarrose, rimose, fibrillose, etc., never sericeous, and rarely hirsute on the margin; odor of *Philadelphus* or gas (as described in subgenus *Sericeicutis)* absent in the species with dry cuticle; mycelium mycorrhizal in probably all species.

Type species: T. flavovirens (Pers. ex Fr.) Lundell apud Lundell & Nannfeldt.

Sect. 9. **LIMACINA** (Fr. ut sect. *Agarici* trib. *Tricholomatis)* Quél. (1872-1873) em. Sing. (1945). *(Equestria* Konr. & Maubl. (1924-1937; *Terrea* Konr. & Maubl. 1924-37). Pileus gray, umber, whitish with grayish fibrils, or golden lemon yellow (or a mixture of these colors); lamellae white, yellowish, gray, or pink, never rusty spotted.

Type species: As in subgenus.

Stirps **Flavovirens** (Pileus viscid, fibrillose, or glabrous; lamellae mostly yellowish); *T. flavovirens* (Pers. ex Fr.) Lundell apud Lund. & Nannf.; *T. sejunctum* (Sow. ex Fr.) Quél. (with several varieties); *T. subsejunctum* Peck; *T. angustifolium* (Murr.) Murr.; *T. Yatesii* (Murr.) Murr.

Stirps **Portentosum** (Pileus viscid, or subviscid, innately fibrillose; lamellae mostly white): *T. portentosum* (Fr.) Quél. and var. *leucoxanthum* Gillet; probably also *T. dryophilum* (Murr.) Murr.; *T. niveipes* Peck; *T. peralbum* (Murr.) Murr.

Stirps **Cingulatum** (a cortina or a membranous veil present): *T. argyreum* (Kalchbrenner) Sing. and closely allied forms or species; *T. triste* (Fr.) Lange; *T. albatum* (Quél.) D'Astis & Maubl.; *T. ramentaceum* (Bull. & Fr.) Ricken sensu Bres.; *T. scalpturatum* (Fr.) Quél. sensu Bres.; *T. Romagnesii* Sing. (T. ramentaceum sensu Romagnesi); *T. cingulatum* (Fr.) Jacobasch.

Stirps **Virgatum** (Taste acrid; spores rather broad; cheilocystidia present): *T. virgatum* (Fr.) Gillet; *T. sciodes* (Secr.) Martin; *T. lilacinocinereum* Metrod; *T. acre* Peck [T. subacre (Murr.) Murr.].

Stirps **Pardinum** (Taste mild; spores large and rather broad): *T. pardinum* Quél.; probably also *T. Cedrorum* R. Maire and *T. terreum* sensu auct. American., e. gr. Kauffm., Murr. p. p. non Fr. (the American species has very narrow spores).

Stirps **Terreum** (Neither cortinate, nor acrid, not viscid; spores rather small) : *T. terreum* (Schaeff. ex Fr.) Quél. and closely related species such as *T. gausapatum* (Fr.) Quél. sensu Bres. (vix sensu Fr.), and *T. subterreiforme* (Murr.) Murr.

Stirps **Atrosquamosum** [Poisonous; positive reaction with formalin usually reddish); stipe often granulose; cheilocystidia usually present] : *T. atrosquamosum* (Chevalier) Sacc. and allied forms (*T. nigromarginatum* Bres.; *T. squarrulosum* Bres., etc.) and *T. orirubens* Quél.; perhaps also *T. luteomaculosum* A. H. Smith (unless this is the type of a closely related stirps).

Sect. 10. GENUINA (Fr.) Sacc. (1887) em. Sing. (1945) (*Citrinofulva* Sing. 1943). Pileus cinnamon, buff, orange, rufous castaneous, chestnut-brown, tawny, etc., or in any of these colors mixed with some pallid or white (resulting in a sordid ochraceous to stramineous effect); lamellae white, buffy pallid, pallid, light yellow, often with rusty, rarely with blackish spots, especially when old; taste more often bitter than acrid, or also mild.

Type species : *T. vaccinum* (Pers. ex Fr.) Quél.) *.

Stirps **Caligatum** (Annulate) : *T. colossus* (Fr.) Quél.; *T. robustum* (A. & S. ex Fr.) Ricken; *T. caligatum* (Viv.) Ricken; *T. matsutake* (S. Ito & Imai) Sing. (Armillaria, S. Ito & Imai); probably also *T. conrelatum* Cooke & Mass. (Armillaria colossa var. australiensis Clel.); *T. ponderosum* (Peck) Sing. (Armillaria, Peck); *T. Murrillianum* Sing. (Armillaria arenicola Murr.).

Stirps **Acerbum** (Stipe furfuraceous or granulose; pileus without reddish or chestnut tinge) : *T. acerbum* (Bull. ex Fr.) Quél. sensu Bres.; *T. psammopodum* (Kalchbrenner) Quél.

Stirps **Imbricatum** (Pileus not distinctly viscid, margin often cortinate, color some kind of reddish brown, chestnut, etc.) : *T. subtransmutans* (Murr.) Murr.; *T. flavobrunneum* (Fr.) Quél. (T. transmutans (Peck) Sacc.); *T. imbricatum* (Fr.) Quél.; *T. inodermeum* (Fr.) Gillet;

* Both the section *Genuina* and the section *Limacina* were introduced by Fries in 1821. In order to conserve these well known sectional names, we have in 1945 attempted to so choose the lectotype of the sections that they may be used for the two most important sections in *Eu-Tricholoma*. If, however, the lectotype of the section *Genuina* as here proposed would be rejected in favor of one of the species constituting the majority of the section in Fries' *Systema*, i. e. the representatives of what we here call *Limacina* (*A. flavovirens*, *A. polyphyllus*, *A. gausapatus*, *A. opicus*, *A. Myomyces*), the name *Citrinofulva* would have to be taken up for sect. 10. The type of the section *Citrinofulva* is *Tricholoma aurantium*.

T. vaccinum (Pers. ex Fr.) Quel. sensu Fr.[88]; *T. arenicola* (Murr.) Murr.

Stirps **Aurantium** (Stipe « subannulate », i. e. with annular zone; context often bitter): *T. albobrunneum* (Pers. ex Fr.) Quél.; *T. rufulum* Heim; *T. aurantium* (Schaeff. ex Fr.) Ricken; *T. subannulatum* (Peck) Sing. (Armillaria, Peck); *T. californicum* (Murr.) Murr. (unless it is too close to the preceding species).

Stirps **Pessundatum** (Stipe not zonate or very indistinctly so; context usually not bitter but often poisonous; spores ellipsoid): *T. pessundatum* (Fr.) Quél.; *T. stans* (Fr.) Sacc.; *T. ustale* (Fr.) Quél. (f. *minor* Fr. cet. excl.); *T. populinum* Lange; *T. Earleae* (Murr.) Murr.

Subgenus VI. **Globulicutis** Sing. (1948) (= *Dermoloma* Lange sensu Sing. 1942). Pileus with hymeniform epicutis consisting of nearly globose cells, consequently forming a monostratous epithelium; pigment dark (microscopically deep gray), incrusting the hyphal walls; clamp connections typically none[89]; odor farinaceous.

Type species: T. atrocinereum (Pers. ex Fr.) Quél. sensu Bres.

Sect. 11. ATROCINEREA Sing. (1948). Characters and type species as in subgenus *Globulicutis*.

T. atrocinereum (Pers. ex Fr.) Quel. sensu Bres.; also *T. cuneifolium* (Fr.) Gillet sensu Metrod, according to the description, not sensu Josserand[90]; obviously also *T. hybridum* Kühner.

[88] *T. vaccinum* (Pers. ex Fr.) Quél. sensu Peck non al. is different from the European species, but it belongs in this same stirps.

[89] Josserand indicates the presence of clamp connections in the trama (*Bull. Soc. Myc. Fr.* **59**: 12. 1943) for his *T. atrocinereum*; no clamps were found in Bresadola's specimens (see Singer, *Lloydia* **5**: 117. 1942). It is possible that two closely related species are hidden in *T. atrocinereum*, or that *T. atrocinereum* occurs in two forms, according to intraspecific differences in sexuality. The latter possibility seems to be more probable.

[90] The species Josserand (*l. c.*) described under the name of *T. cuneifolium* is, in the author's opinion, not as closely related to *T. atrocinereum* as Josserand assumes, and as one would be inclined to believe when observing all the misdeterminations in the literature. However, as has been said by Kühner, the characters of the cuticle are sometimes of secondary importance, and a similar epicutis can be found in *Pluteus*, *Calocybe*, and other genera. *T. cuneifolium* is known to the author only from the literature, and it is thought to be preferable not to insert a new genus (or rather *Dermoloma* in a new status) at present for the group containing the *Tricholoma cuneifolium* of Josserand (and evidently Lange). See also p. 250.

KEY TO THE SPECIES

For reasons given in the paragraph on « State of Knowledge » (p. 222), the insertion of a new key to the species of *Tricholoma* would not help materially in the determination beyond the usefulness of the keys already in existence (Lange, Métrod, for European species ; Kauffman and *North American Flora* for U. S. A.).

24. PODABRELLA Sing.

Lloydia **8** : 143. 1945

Type species : Collybia microcarpa (Berk. & Br.) Hoehnel sensu Hoehnel.

Syn. : Termitomyces subgen. *Praetermitomyces* Heim, *Arch. Mus. Nat. Hist. Nat.* VI ser. **18** : 147. 1941.

Characters : Habit of the carpophores mycenoid-collybioid ; pileus with an epicutis consisting of thin, repent, parallel, hyaline, smooth, filiform hyphae; hypodermium consisting of somewhat thicker hyphae which are contracted at the septa, likewise hyaline (the whole fungus with very little or no pigment) and elongate ; lamellae subfree to adnate, thin, intermixed with lamellulae ; spore print pale rose color in the type species, probably white or nearly so in other species ; spores hyaline under the microscope, smooth, rather thin-walled, nonamyloid, ellipsoid to ovoid ; basidia rather small, normal in all regards, 4-spored ; cystidia usually none ; edge of the lamellae homomorphous ; trama of the hymenophore regular ; stipe solid, rather thin, without distinct pseudorrhiza, rather soft, rising from small globulose white bodies which are ejected from termite nests by the termites [these bodies represent the primordium of the species « mycotêtes », according to Heim)], or from a mat of sparse white mycelium on decayed wood ; context fleshy, unchanging ; consisting of hyphae which are devoid of clamp connections, nonamyloid.

Development of the carpophores : P. microcarpa is most probably hemiangiocarpous, certainly not gymnocarpous (according to Heim).

Area : North America, Tropical Africa and Asia.

Limits : This is clearly separated from *Termitomyces* by the absence of a pseudorrhiza, by the almost complete or complete absence of pigment, by the absence of cystidia in virtually all collections, and

by the regular trama [21]. There are no difficulties of delimitation regarding the other genera of the *Tricholomataceae*.

State of knowledge : The type species has been extensively studied by R. Heim in Africa, and the American species is completely known except for the exact color of the spore print [22] and the development of the carpophores. Other species are not known at present.

Practical importance : It had been believed that *P. microcarpa* plays an important rôle in the nutrition of the termites in the palaeotropics, and thus might have some indirect practical importance, when R. Heim restudied this relationship between fungus and termite, and came to the conclusion that the termites are compelled to rid their nests of this « Hausschwamm », and use it only occasionally for food ; the larvae are not fed fungi at all. The practical importance of these fungi, consequently, consists entirely in its value for human consumption. It is thought to be one of the most delicious edible fungi of the regions where it is common, and by some it is considered to be superior to all other species. The American species, on the other hand, does not seem to have any practical importance at all.

SPECIES

P. microcarpa (B. & Br.) Sing. (Entoloma, Sacc. ; Collybia, Hoehnel; Gymnopus, Van Overeem); *P. alba* (Peck) Sing. (Collybia, Peck).

25. PLEUROCOLLYBIA Sing.

Mycologia **39** : 81. 1947.

Type species : Pleurocollybia praemultifolia (Murr.) Sing.

Characters : Habit of the carpophores collybioid pleurotoid ; pileus

[21] The trama of the lamellae of young carpophores is regular in *P. alba*, and is also regular in the youngest available fruiting bodies of the type species in dried material. If the very young hymenophore of *P. microcarpa* should prove to be bilateral rather than regular, it may still be allowed to consider *Podabrella* as an autonomous genus — in consideration of the other characters distinguishing it from *Termitomyces* — yet, it would become necessary to transfer the genus to the *Amanitaceae*. This would leave *P. alba* quite isolated in the *Tricholomataceae*, and a new generic name would have to be proposed for this single species. The decision on this question must be left for further investigation.

[22] The spore print of *P. alba* is white or nearly so in moderately thick layer. However, the author does not know if this would hold true for more numerous

much like that of a *Collybia* in shape; its cuticle consisting of colored parallel to subparallel, horizontal, filamentous hyphae, dense; lamellae crowded, emarginate adnexed, narrow, thin; spores pure white in print; hyaline under the microscope (also in dried condition), with thin to moderately thin wall, smooth, nonamyloid, subglobose, extremely small (around 3 µ); basidia very small but otherwise normal; cystidia of any kind absent; hymenophoral trama rather thin, rather regular, hyaline; subhymenium subcellular; stipe strongly eccentric and oblique, well developed but rather thin as in *Collybia*; context consisting of hyphae with moderately thin to moderately thick walls which are nonamyloid; clamp connections absent; septa crowded and often narrower than the diameter of the hyphae at the widest point; on rotten wood.

Development of the carpophores: Unknown.

Area: Florida (probably with a larger distribution).

Limits: This genus differs from *Tricholoma* by its lignicolous habit, its strongly eccentric and oblique stipe, the excessively small spores, and, in addition, by a combination of characters uncommon in *Tricholoma*. It differs from *Podabrella* in the strong pigmentation of the cuticle of the pileus, the smaller spores and the eccentric and oblique stipe. It differs from *Callistosporium* in the perfectly hyaline spores and hyphae in ammonia mounts from dried material and also in the smaller size of the spores; in addition it differs in the habit which is somewhat pleurotoid in *Pleurocollybia* (stipe oblique and eccentric) which is never the case in *Callistosporium*.

State of knowledge: The only species is completely known except for its cytology and manner of development.

Practical importance: Hardly any.

SPECIES

P. praemultifolia (Murr.) Sing. (Gymnopus, Murr.).

26. CALLISTOSPORIUM Sing.

Mycologia 36: 363. 1944.

Type species: *Gymnopus Palmarum* Murr. [= *Callistosporium Palmarum* (Murr.) Sing.].

Characters: Habit of the carpophores collybioid; pigment present, abundant, changing its color in dried condition, mostly concentrated

in solid (or sometimes dissolved) pigment bodies inside the spores, and also often in other elements of the hymenophore where the pigment is colorless under the microscope in fresh condition but precipitates on dehydration; pileus hygrophanous or non hygrophanous, its cuticle consisting of repent, elongate hyphae; hymenophore lamellate, lamellae broadly or narrowly adnexed or emarginate; spore print white when fresh; spores ellipsoid, smooth, nonamyloid, at least a certain percentage of the spores usually partly bright colored (the interior of the spores) in dried specimens, or rarely with a hyalino pigment body, with thin, hyaline walls; basidia normal but sometimes some of them pigmented the same way as the spores; cystidia of all types absent; hymenophoral trama regular, nonamyloid; stipe central, thin, fleshy fragile, to subcartilaginous; context not tough, nor reviving, consisting of hyphae without clamp connections. On the base of palm trees and on various kinds of wood, also on *Sphagnum*.

Development of the carpophores: Not studied.

Area: In the Asiatic subtropics and in America from the subtropics to the boreal zone (Canada).

Limits: The peculiar pigmentation of the spores, if it can be considered as constant, is undoubtedly an easy way of recognizing this genus among all other genera of agarics. However, even if additional species should be discovered where this pigmentation is either not present or not constant, the genus *Callistosporium* would still be distinguishable from *Tricholoma* by its habit, from *Podabrella* by the pigmentation of the hyphae, and from *Pleurocollybia* by the central, straight stipe and larger spores. The delimitation of *Callistosporium* does therefore not seem to represent a problem.

State of knowledge: Our knowledge of the species is very satisfactory. However, it may be expected that not all the species actually belonging to *Callistosporium*, have yet been recognized as such. This is probable because, without careful examination of dried material and data on the absence of clamp connections, specimens are likely to be misinterpreted as belonging to such large genera as *Collybia*, *Marasmius*, « *Galera* », *Gymnopilus*, « *Psilocybe* », etc. where the types as well as the descriptions remain buried unless systematic attempts are made in order to redefine the older species in these genera. This was demonstrated in the case of *Collybia luteoolivacea* and *C. colorea*. Thus far only four species have been described in or transferred to *Callistosporium*.

SPECIES

C. Palmarum (Murr.) Sing. (Gymnopus, Murr.); *C. Heimii* (Sing.) Sing; *C. luteoolivaceum* (Berk. & Curt.) Sing. (Collybia, Sacc.; Collybia colorea Peck; Callistosporium Psalocybe Murr. & Sing.); *C. galerinoides* Sing.

KEY TO THE SPECIES

A. Old World species (subtropical-montane zone of the south slope of the Caucasus, on wood of *Taxus baccata*); pigment of the spores dark bluish lilac. *C. Heimii*

A. Species occurring in the Western Hemisphere; pigment of the spores purple or red, rarely absent.

B. Spores 7.5-8.7 × 4-5.2 μ; carpophores growing on the base of palms. *C. Palmarum*

B. Spores smaller; carpophores growing on trunks and buried wood of trees other than palms, or on *Sphagnum* moss

C. On *Sphagnum*. General appearance like that of a *Galerina*. *C. galerinoides*

C. On wood. General appearance like that of a *Collybia* or *Gymnopilus*. *C. luteoolivaceum*

GENERA IMPERFECTLY KNOWN

Coolia Huysman, *Med. Nederl. Myc. Ver.* 28: 51. 1943 (= *Squamanita* Imbach). These are fungi of the general appearance of a *Tricholoma* but with double veil forming very conspicuous scales on the bulbous base. The type species of *Coolia* is a species first described by Miss Cool as *Lepiota odorata* Cool, and later transferred to *Coolia* as *C. odorata* (Cool) Huysman. Since it appears to be rather probable that *Squamanita Schreieri* Imbach (*Mitt. Naturf. Ges. Luzern*, 15: 81. 1947) is closely related and almost certainly congeneric with *Coolia*, we shall discuss the two genera here as synonyms. As for their characters, one may take it for granted that the spores are nonamyloid as indicated by Schreier. The picture published by Imbach (fig. C) does not make it clear whether the Swiss species has regular trama, but Schreier calls it « normal » which may mean that it is regular. Material received by this author from Holland thanks to the kindness of Miss Van der Laan, Amsterdam, shows regular trama and numerous clamp connections in the epicutis which consists of a cutis of parallel dark colored hyphae. Imbachs figure does not

show clamp connections, and one cannot be sure whether this means that they are absent, or have been overlooked. No cytological or chemical characters are available. Not knowing the type specimen of either genus, and without a firsthand knowledge of fresh material, this author is reluctant to accept *Coolia* as a valid genus, and is equally doubtful about its identity with *Tricholoma*, a section of which it becomes in the treatment of Konrad & Maublanc (1948). Although this latter solution may be very close to the best possible disposal of the genus, the presence of clamp connections in my Dutch material, in combination with the strongly developed veil, make *Coolia* at least a strongly aberrant group in *Tricholoma*.

Tribus LEUCOPAXILLEAE Sing.

Sydowia **2** : 29. 1948

Type genus : Leucopaxillus Boursier.

Characters : Habit of the carpophores clitocyboid or tricholomatoid, more rarely pleurotoid; spores amyloid; trama amyloid or non-amyloid; hyphae with or without clamp connections; gelatinous layers none; hymenophoral trama non bilateral, subirregular to regular; cheilocystidia present or absent; macrocystidia present or absent; leptocystidia present or absent; metuloids, gloeocystidia, setulae none; cuticle of the pileus not consisting of a well differentiated epicutis that is made up of diverticulate hyphae, or dermatocystidia (other than occasional dermatopseudocystidia), or broom cells, etc., epicutis not cellular (but see genus *Dermoloma*); veil none, or very slightly developed (in *Melanoleuca*); on the soil, on wood, rarely on grass roots, ant hills, etc.

KEY TO THE GENERA

A. Spores either smooth, or, if warty, devoid of a suprahilar smooth disc (plage); clamp connections present or absent.

B. Spores ellipsoid oblong to fusoid-cylindric or short cylindric, more rarely ellipsoid-ovoid, distinctly amyloid, smooth ; clamp connections present or absent ; lamellae in most species distinctly decurrent, often forked ; pileus with moderately thick flesh, never tough and reviving, hygrophanous, or non-hygrophanous, usually dusky colored, or with a cinnamon tinge (if cheilocystidia prominent, see also genus *Hebeloma*).

27. *Cantharellula*

B. Spores short ellipsoid to subglobose, warty, or, if smooth, often very

slightly amyloid [73] (yet, if warty, very strongly amyloid); clamp connections always present; lamellae distinctly decurrent, or sinuate-adnexed, adnate, emarginate, etc.; pileus often rather thick, fleshy or tough and sometimes reviving, non hygrophanous, or rarely with hygrophanous spots, not dusky-colored

C. Pseudocystidia (macrocystidia) none; lamellae usually with entire edges; hyphae nonamyloid, carpophores rarely distinctly pleurotoid. 28. *Leucopaxillus*

C. Pseudocystidia (macrocystidia) present; lamellae usually distinctly serrulate-crenulate; all hyphae, or some of them, usually distinctly amyloid; carpophores often distinctly pleurotoid. 29. *Lentinellus*

A. Spores warty or minutely subpunctulate, with plage, clamp connections none 30. *Melanoleuca*

27. CANTHARELLULA Sing.

Ann. Mycol. 34: 331. 1936

Type species: Cantharellula umbonata (Gmelin ex Fr.) Sing.

Syn.: Omphalius Roussel ex Earle, *Bull. N. Y. Bot. Gard.* 5: 432. 1909 (ex spec typ. prop.) [74].

Characters: Habit of the carpophores clitocyboid, more rarely so slender it may also be characterized as almost omphalioid, rarely tricholomatoid; pigment either dissolved in the cell sap or incrusting it, present in all species known; pileus fleshy but rather thin in most species, with a superficially appressed, radial fibrillosity, or without it, opaque to almost subtomentose, often rimulose, or entirely glabrous and smooth and then often hygrophanous, non striate or slightly pellucidostriate in moist condition at the margin, convex to deeply infundibuliform; epicutis consisting of elongate ordinary hyphae, not cellular; lamellae adnate, or subdecurrent, or decurrent,

[73] If smooth and strongly amyloid see under *Lentinellus* (if epicutis non cellular), and under *Dermoloma* (if cuticle strongly cellular).

[74] *Omphalius* is merely a variation of the ordinary spelling *Omphalia* (Pers.) Gray and cannot, therefore be claimed to be a different genus. Aside from that, it is as Earle himself observed, too close to other similar generic names, leading to unending confusion, and has therefore to be excluded since it is a typical candidate for the list of nomina ambigua according to the International Rules, Art. 62. It may also be questioned whether Earle who meant the genus *Omphalius* to combine the sections *Infundibuliformes* and *Cyathiformes* had the right to propose as the type species a species from the section *Cyathiformes* rather than from the *Infundibuliformes* but since this combination of sections is his own emendation, the proposed type is probably acceptable

sometimes strongly sinuate, most frequently distinctly and often deeply decurrent, close to distant, often more or less forked, sometimes repeatedly forked, often colored, more rarely white, often developing cyanic acid (Subg. V.); spore print pure white [1]; spores hyaline, smooth, distinctly amyloid, cylindric or ellipsoid oblong, or short cylindric-subellipsoid, rarely ellipsoid ovoid, never with both the inner and outer side convex and the quotient of length and breadth smaller than 2; basidia normal but sometimes comparatively long, usually 4-spored; cheilocystidia in some species present but very scattered and somewhat inconstant, inconspicuous; cystidia otherwise not present; hymenophoral trama subregular (*C. cyathiformis*), or subirregular to almost intermixed; subhymenium distinctly cellular to subcellular intermixed; stipe central, neither tubular nor truly cartilaginous but fleshy to fleshy fibrous; veil none; context unchanging, or in some species reddening; clamp connections present or absent; tissues becoming purplish with iodine in *C. umbrosa* according to Smith & Walter, otherwise becoming pale yellow (nonamyloid) in Melzer's reagent. On the soil, or on wood.

Development of the carpophores : Unknown.

Area : Temperate zones; some species reach high altitudes in the mountains, and in the boreal zone (north into the subarctic zone); one species in the American subtropics.

Limits : This genus consists of several subgenera that are closer to each other than to any of the other agarics. Some of the subgenera have certain affinities outside the genus *Cantharellula.*

(1) The genus *Pseudohygrophorus* is undoubtedly close to *Cantharellula.* As for the separation between these two genera see under *Pseudohygrophorus.*

(2) *Xeromphalina* is close to the subgenus *Pseudoomphalina.* In fact, the author considered (1942) another solution, viz. the incorporation of *Pseudoomphalina* in *Xeromphalina* rather than in *Cantharellula.* However, the absence of cystidia, the fleshier character of the stipe, the absence of basal tomentum, and the inconstant incrustation of the hyphal walls are strong arguments in favor of *Cantharellula,* and they can also be considered as the characters separating the two genera.

(3) *Leucopaxillus,* sect. *Aspropaxilli* differs in thicker, fleshier pilei, less strongly amyloid and at the same time shorter spores, and by

[1] In a 60 year old spore print of *C. cyrophila* found to be salmon color.

combinations of characters not occurring in any of the subgenera of *Cantharellula*.

(4) *Armillaria* and *Catathelasma* can be distinguished by the divergence of the hyphae of the hymenophoral trama in young specimens; the former also by the deeply emarginate lamellae, and the latter in being very thick and fleshy, both in being veiled.

(5) *Dermoloma*, see there (p. 250).

State of knowledge: The species indicated here are all well known except for their development. But several more species may eventually be found to belong here since there are many species of *Clitocybe* and *Omphalia* left that have not yet been tested as for their iodine reactions. This possibility has to be kept in view when the strong hiatus between the subgenera constituting the genus *Cantharellula* is evaluated. It is quite possible that these gaps will eventually be filled in by species not now known to belong in *Cantharellula*. The subdivision of *Cantharellula* was undertaken on the basis of the knowledge of not more than ten species.

Practical importance: Some of the species are edible but of minor importance except for local use in certain regions.

SPECIES

Subgenus I. **Eucantharellula** Sing. (1943). Pileus opaque, subvelutinous, non hygrophanous; lamellae strongly forked and strongly decurrent, narrow, white or pink; context often reddening when bruised; clamp connections present; hymenophoral trama strongly interwoven but in young specimens predominantly axillarly arranged, with many of its hyphae running parallel or subparallel; subhymenium subirregularly intermixed subramose, its elements short, strongly interlaced curved (in all directions), and therefore often appearing cellular; pigment gray, dissolved. Among mosses.

C. umbonata (Gmelin ex Fr.) Sing. [Merulius, Pers.; Cantharellus, Fr.; Clitocybe, Konrad; Cantharellus muscoides (Wulfen ex Schroeter); Cantharellus dichotomus Peck], and f. *roseolamellata* Sing.

Sugenus II. **Pseudoarmillariella** Sing. (1948). Pileus opaque, appressedly fibrillose-subpunctulate in a radial arrangement, hygrophanous, with parallel or subparallel radially arranged hyphae making up the cuticle; pigment incrusting; context not reddening when bruised; clamp connections present; lamellae strongly de-

current and rather distinctly forked; hymenophoral trama subirregular, its hyphae interwoven; subhymenium as in the preceding subgenus (1). On decayed wood.

C. ectypoides (Peck) Sing.

Subgenus III. **Pseudotricholoma** Sing. (1948). Pileus opaque, subvelutinous, non hygrophanous, non fibrillose; lamellae neither strongly forked nor strongly decurrent, rather broad at the stipe; context often reddening when bruised; clamp connections present, otherwise similar to subgenus I.

C. umbrosa (A. H. Smith & Walter) Sing. (Tricholoma, Sm. & Walter).

Subgenus IV. **Pseudoomphalina** Sing. (1948). Pileus not quite opaque, glabrous, hygrophanous or almost so, non fibrillose, the cuticle consisting of radially arranged, subparallel to parallel, smooth hyphae which are slightly or strongly incrusted, or non incrusted by the pigment; pigment macroscopically dull ochraceous to alutaceous-buff or orange buff, clay color or deep cinnamon or umbrinous; context not reddening when bruised but sometimes colored almost as deep as the surface when wet; clamp connections present; hymenophoral trama irregularly arranged (though a majority of its hyphae is more or less axillarly arranged) and strongly interwoven and variable in size and shape; subhymenium as in subgenus I. On earth and on charcoal.

Type species: C. Kalchbrenneri (Bres.) Sing.

C. Kalchbrenneri (Bres.) Sing. (Omphalia, Bres.; Xeromphalina, Sing. 1942; Omphalia graveolens Petersen; Clitocybe farinacea Murr.); *C. felloides* (Kauffm.) Sing. (Clitocybe, Kauffm.; C. felea var. glareosa Kauffm. see A. H. Smith); *C. intermedia* (Kauffm.) Sing. (Clitocybe, Kauffm.); probably also *C. umbrinopurpurascens* (Maire) Sing. (*Clitocybe*, Maire).

Subgenus V. **Pseudoclitocybe** Sing. (1943). Pileus not quite opaque, glabrous or somewhat radially fibrillose, strongly hygrophanous, its cuticle consisting of subparallel hyphae which are radially arranged and pigmented with a fuscous pigment which is either predominantly incrusting, or predominantly intracellular; lamellae usually more or less forked, usually more or less deeply decurrent, rather narrow to rather broad; context not reddening when bruised; clamp connections absent in the carpophores; hymenophoral trama rather regular, at least near the edge of the lamellae, consisting of rather broad hyphae which are not incrusted by the pigment, towards the

back of the lamellae becoming rather irregular in age; subhymenium cellular. On earth and on foliage, also on wood-débris and on decayed stumps and logs, needle beds, etc., also among deep moss.

Type species: *C. cyathiformis* (Bull. ex Fr. p. p.) Sing.

C. cyathiformis (Bull. ex Fr. p. p.) Sing. (Clitocybe, Quel.); *C. obbata* (Fr.) Bousset (Clitocybe, Quel.); *C. oregonensis* (Murr., Sing. (Clitocybe, Murr.); *C. coprophila* (Speg.) Sing. (Clitocybe, Speg.).

KEY TO THE SPECIES

A. Clamp connections present.

B. Pileus non hygrophanous, very opaque, even when wet, subvelutinous or minutely rimulose; flesh usually reddening when bruised.

C. Lamellae narrow near the stipe (and everywhere), repeatedly forked rather obtuse at the edge when young, decidedly decurrent. *C. umbonata*

C. Lamellae rather broad at the stipe, not much forked, with acute edges, sinuate to subdecurrent. *C. umbrosa*

B. Pileus subhygrophanous, not always opaque when wet, radially fibrillose or completely glabrous and never rimulose; flesh never reddening when bruised.

D. Pileus ochre gray, distinctly fibrillose and somewhat punctate when fresh and young; odor not remarkable; on coniferous wood. *C. ectypoides*

D. Pileus sordid ochre alutaceous to orange alutaceous or rather deep cinnamon, fibrillose only at the margin (slightly), or entirely glabrous; odor farinaceous or of cucumber; on the ground in woods.

E. Pileus dull alutaceous to carneous alutaceous, with a slight transparent striation at the margin in moist condition, smooth when dry; lamellae subdistant to distant when mature; base of stipe without distinct rhizomorphs, about 2 mm broad. Temperate species. *C. Kalchbrenneri*

E. Pileus more richly colored, or base of stipe with rhizomorphs and broader than 2 mm., and margin estriate.

F. Pileus « clay color » (Ridgway) when moist (if umber cf. *C. umbrinopurpurascens* of Europe); stipe with rhizomorphs. Eastern United States to Michigan. *C. felloides*

F. Pileus more cinnamon when moist; stipe without distinct rhizomorphs which are white. Western United States. *C. intermedia*

A. Clamp connections none in the carpophore tissues (they may be present in the mycelium). *C. cyathiformis, C. oregonensis, C. obbata, C. coprophila*

28. LEUCOPAXILLUS Boursier

Bull. Soc. Myc. Fr. **41**: 391. 1925, em. Singer, *Rev. Mycol.* **4**: 69. 1939.

Type species: *L. pseudoacerbus* (Cost. & Duf.) Boursier [= *L. tricolor* (Peck) Kühner].

Syn.: *Aspropaxillus* Kühner & Maire. *Bull. Soc. Mycol. Fr.* **50**: 13. 1934.

Characters: Habit of the carpophores clitocyboid, tricholomatoid, or very rarely somewhat pleurotoid; pileus opaque, non-hygrophanous, rarely with hygrophanous spots, not viscid, with smooth or short ribbed to crenate, initially involute margin, thick, fleshy but not watery; cuticle little differentiated; lamellae decurrent, or sinuate, or emarginate sinuate, or adnexed to adnate; often developing cyanic acid (sect. I); spore print pure white; spores (Pl. XXIII, 1-6) hyaline, rough to warty without suprahilar plage, or smooth, and then very slightly (even inconstantly) amyloid (but the species with warty spores strongly amyloid because of the episporium causing the ornamentation above an otherwise smooth wall), rather small to medium sized (up to 10 μ long), rather short ellipsoid, subglobose, ovoid; basidia normal in all regards; cystidia none; cheilocystidia, however, sometimes differentiated but small and not very conspicuous; hymenophoral trama regular to subirregular (more irregular in age); subhymenium ramose (filamentous), thin; stipe central, very rarely eccentric, usually thick and fleshy to somewhat tough; veil none; pigment intracellular, or incrusting in the cuticle of certain species (Pl. XXIII, 7), macroscopically often bright colored, in some species wanting; context unchanging on bruising; its hyphae nonamyloid and with numerous clamp connections. On humus and débris, especially foliage, needle beds, even anthills.

Development of the carpophores: Gymnocarpous (« decidedly gymnocarpous » in *L. albissimus* var. *paradoxus* according to Kühner).

Area: Boreal to subtropical zones in the northern as well as in the southern hemisphere.

Limits: Since all characters excepting the strongly amyloid episporium are identical in section *Aspropaxilli* and in *Eu-Leucopaxilli*, Singer (1939) and Singer & Smith (1943) have not followed Kühner & Maire who separated the species without episporium from the main genus *Leucopaxillus* as an autonomous genus. Metrod (1939) has combined the genera *Leucopaxillus* and *Melanoleuca* under the

common name *Melanoleuca*, claiming that there are no constant differences between the two genera. The author disagrees with Métrod's observations. The genus *Melanoleuca* is constantly different from *Leucopaxillus* in the absence of clamp connections which are always plentiful in *Leucopaxillus*. The plage on the spores of *Melanoleuca* is almost as good a character but not always easy to demonstrate, especially in those species that have a very slightly developed episporium. The inconstance of the leptocystidia in *Melanoleuca* has been indicated before by Heim and Singer, but Josserand has added a new character distinguishing the two genera, viz. the angular shape of the spores of *Melanoleuca* when seen from one end (in vertical position) after chemical removal of the episporium. Kühner has shown that there is a pigment formation in *Melanoleuca* that does not occur in *Leucopaxillus*.

There are no other problems in the delimitation of *Leucopaxillus* which is a remarkably well defined and very homogeneous genus.

State of knowledge : The genus has been monographed recently, and the knowledge of the species is nearly complete. In their monograph, Singer & Smith distinguished 18 species and varieties; in addition, 1 variety and 1 new species have been discovered since then, which brings the number of autonomous species up to 13.

Practical importance : *Leucopaxillus giganteus* and *L. candidus* have been mentioned in some European papers as a new source of an antibiotic substance named « clitocybine » with a potential application against tuberculosis.

SPECIES

Sect. 1. **ASPROPAXILLI** (Kühner & Maire) Sing. & Sm. (1943). Spores smooth, slightly amyloid (Pl. XXIII A, 3).

Type species : L. giganteus (Fr.) Sing.

L. candidus (Bres.) Sing. (Clitocybe, Bres.); *L. giganteus* (Fr.) Sing. (Clitocybe, Quél.; Paxillus, Fr.; Aspropaxillus, Kühner & Maire; Melanoleuca oreades Murr.) *L. septentrionalis* Sing. & Sm.; *L. lepistoides* (Maire) Sing. (Tricholoma, Maire; Aspropaxillus, Kühner & Maire).

Sect. 2. **EU-LEUCOPAXILLI** Sing. & Sm. (1943) (*Typici* Sing. 1943). Spores rough from a warty episporium which is very strongly amyloid (Pl. XXIII, 1-2, 4-6).

Type species : L. pseudoacerbus (Cost. & Duf.) Boursier.

L. albissimus (Peck) Sing. [Clitocybe, Sacc.; Clitocybe subhirta (Peck) Peck; Tricholoma lentum (Post apud Romell) Sacc.; Lepista barbara Maire; Clitocybe paradoxa Cost. & Duf.; Clitocybe albiformis Murr.; Clitocybe stipitata Murr., these synonyms belong to the type variety and eight other varieties of this species]; *L. nauseodulcis* (Karst.) Sing. & Sm. (Clitocybe, Karst.; Pleurotus, Sacc.); *L. pulcherrimus* (Peck) Sing. & Sm. (Clitocybe, Peck); *L. laterarius* (Peck) Sing. & Sm. (Tricholoma, Sacc.); *L. rhodoleucus* (Romell) Kühner (Clitocybe, Sacc.); *L. tricolor* (Peck) Kühner (Tricholoma pseudoacerbum Cost. & Duf.; Leucopaxillus, Boursier); *L. brasiliensis* (Rick) Sing. & Sm.; *L. amarus* (Alb. & Schw. ex Fr.) Kühner; [Tricholoma, Rea; Lepista, Maire; Clitocybe gentianea Quél.; Clitocybe vulpecula (Kalchbr.) Sacc., Melanoleuca bicolor Murr.; Melanoleuca roseibrunnea Murr.] with several forms and var. *gracilis* (Kalchbr.) Sing. & Sm.); *L. gracillimus* Sing. & Sm. with var. *Rappii* (Murr.) Sing. (Clitocybe Rappii Murr.).

KEY TO THE SPECIES

A. Spores smooth, slightly amyloid.

B. Lamellae decurrent, lamellulae not abruptly rounded; stipe not grayish in old specimens or in properly prepared dried material; lamellae arcuate and rather narrow.

C. Lamellae white, eventually becoming merely sordid or pallid; old pilei whitish. Known with certainty only from the large mountain ranges of the eastern hemisphere. *L. candidus*

C. Lamellae, if white at first, soon with a creamy or buff tint and eventually becoming almost alutaceous; old pilei cream buff to chamois. *L. giganteus*

B. Lamellae mostly and at least partly sinuate or emarginate; lamellulae rather abruptly rounded; stipe grayish in old specimens and or in well dried herbarium specimens; lamellae subventricose in the marginal third, rather broad.

D. Pileus colored from the start; context never blue. Northern part of North America, from Ontario to Oregon. *L. septentrionalis*

D. Pileus at first white; context sometimes blue within the base, the blue spots turning yellow in H_2SO_4. North Africa. *L. lepistoides*

A. Spores with a warty, strongly amyloid episporium.

E. Cheilocystidia scattered or absent, pigment of the pileus absent or not incrusting the walls of the hyphae of the cuticle with dark reddish brown areolae, warts, or rings.

F. Lamellae white, rarely yellow or pinkish, never becoming vinaceous to purplish brown in the herbarium.

G. Pileus without hygrophanous spots.

H. Pileus never with a pinkish flush and never bright yellow, but pure white to cream color or pale buff, pale tan, etc.; at least some of the mature spores measuring longer than 5.5 μ.

I. Stipe central and not exceedingly long, not on anthills. Temperate zones. *L. albissimus*

I. Stipe eccentric and very long, arising from anthills; taste sweetish but disagreeable. Finland. *L. nauseosodulcis*

H. Pileus not colored as indicated above, or spores smaller.

J. Pileus, stipe, and context under the cuticle yellow; spores 4-5.8 μ long. Temperate zone. *L. pulcherrimus*

J. Pileus, stipe and context not yellow; spores never larger than 5.5 μ. *L. laterarius*

G. Pileus with hygrophanous spots when fresh; lamellae at first pinkish or pinkish white. Sweden to North Africa. *L. rhodoleucus*

F. Lamellae distinctly yellow, pale yellow, sulphur or cream color, becoming vinaceous or purplish brown in the herbarium.

K. Pileus dark violet, ashy green around the margin. Brazil. *L. brasiliensis*

K. Pileus pinkish buff to dull tan. Temperate species. *L. tricolor*

E. Cheilocystidia numerous; hyphae of the cuticle of the pileus more or less incrusted by a brown or reddish brown pigment which forms warts, areolae, or rings on the walls (hyphae rarely not incrusted).

L. Stipe 8 mm. or more broad; lamellae close to crowded. Temperate zone. *L. amarus*

L. Stipe less than 8 mm. broad; lamellae extremely crowded. Subtropical zone. *L. gracillimus*

29. LENTINELLUS Karst.

Bidr. Finl. Folk 32 : xvii. 1879

Type species : Lentinellus cochleatus (Fr.) Karst.

Syn. : Hemicybe Karst., *l. c.*, p. xviii, 1879.
Lentinellus Fayod, *Prodr.*, *Ann. Sc. Nat. Bot.*, VII, 9 : 336, 1889.
Lentinaria Pilát, *Ann. Mycol.*, 39 : 73, 1941, nom. nud.

Characters : Habit of the carpophores clitocyboid-pleurotoid or omphalioid-pleurotoid, or plainly pleurotoid; pileus stipitate or sessile; lamellae usually more or less serrulate-crenulate; spore print white or whitish; spores small, globose, subglobose, or ovoid, or very broadly ellipsoid, finely rough, verruculose, or almost smooth to smooth, strongly amyloid; basidia normal in all regards; macrocystidia or at

least occasional ends of oleiferous hyphae entering the hymenial layer, no other form of cystidia present; hymenophoral trama subregular to subirregular; or almost intermixed in age; stipe either eccentric or fasciculate or absent; veil none; context rather tough, somewhat reviving, often with strong aromatic odor, often acrid to the taste, the tissue frequently made up of partly amyloid hyphae, with clamp connections, and rather numerous oleiferous hyphae; many of these elements with thick walls. On freshly cut or decayed wood, and on grass roots.

Development of the carpophores: Gymnocarpous in *L. omphalodes* (according to Kühner); hymenium originally formed at the lower surface of the carpophore in *L. omphalodes*, on the upper surface in *L. ursinus* (according to Kühner).

Area: Nearly cosmopolitan.

Limits: This genus is undoubtedly most closely related to *Leucopaxillus* yet sufficiently separated from the latter genus by its habit, its anatomy, and its chemical characters. Pilát proposes to separate the group of species with rough spores from the remainder of the species, and proposes a new generic name *(Lentinaria)* for the former. The author believes that this would result in an artificial division.

State of knowledge: Most of the species are well known, yet it may be that many more *Lentinelli* are hiding among the innumerable species of *Lentinus* described in the literature. These species can be transferred only after a careful analysis of the spore characters of the type specimens. At present, we distinguish not more than ten species.

Practical importance: Some of the species of *Lentinellus* are wood-destroyers. Some are edible.

SPECIES

Sect. OMPHALODEI Sing. (1943) (*Lentinus* sect. *Lentinaria* Pilát 1946). Spores distinctly verruculose-rough; odor none, or wine-like; pileus umbilicate, usually not densely cespitose; lamellae distant to moderately close.

Type species: *L. omphalodes* (Fr.) Karst.

L. tridentinus (Sacc. & Syd.) Sing. (Lentinus badius Bres. non Berk.; Lentinus tridentinus Sacc. & Syd. in Sacc.); *L. flabellinus* (Quél.) Konr. & Maubl. (Lentinus, Quél.); *L. omphalodes* (Fr.) Karst. (Lentinus, Fr.); *L. bisus* (Quél. apud Bres.) Kühner & Maire (Lentinus,

Quél.); *L. semivestitus* (Peck) Sing. (Tricholoma, Sacc.); *L. americanus* (Peck) Sing. (Lentinus, Peck); *L. umbilicatus* (Peck) Sing. (Lentinus, Peck) unless too close to *L. omphalodes*.

Sect. 2. COCHLEATI (Fr. ut sect. *Lentinorum*, sensu str.) Sing. (1943). Spores smooth or very slightly roughened; odor of young specimens strongly of anise, more rarely absent; stipes fasciculate; pileus medium to large (30-70 mm in diameter) with rather thick and tough context; lamellae subclose to crowded.

Type species : L. cochleatus (Pers. ex Fr.) Karst.

L. cochleatus (Pers. ex Fr.) Karst. [Lentinus, Pers. ex Fr.; Lentinellus cornucopioides (Bolt. ex Schroet.) Murr.]; probably also *L. pallidealutaceus* (Henn.) Sing. if the spores are indicated correctly by Hennings.

Sect. 3. PLEUROTI (Fr. ut sect. *Lentinorum*, sensu str.) Sing. (1943). Spores smooth to very slightly roughened; lamellae subclose to crowded; odor of wine, or none; stipe none.

Type species : L. ursinus (Fr.) Kühner.

L. ursinus (Fr.) Kühner (Lentinus, Fr.); *L. vulpinus* (Fr.) Kühner & Maire sensu Kühner & Maire (non Ricken) (Lentinus, Fr.).

KEY TO THE SPECIES

A. Carpophores stipitate.

B. Stipes in groups of 2-4, or singly; pileus up to 40 mm in diameter; odor of wine, or none, not of anise; lamellae distant to moderately close

C. Growing on roots of *Gramineae* in Kansas .... *L. semivestitus*

C. Growing on wood or detritus in woods.

D. Stipe without deep longitudinal furrows, short, sometimes absent

E. On *Sorbus* (and perhaps other frondose trees), pileus 5-10 mm broad, brown, then expallent. Alps, Macedonia, and Caucasus. .... *L. tridentinus*

E. On branches of conifers, also other trees, or on the ground in woods; pileus larger, paler

F. Stipe not or slightly eccentric, 10-15 × 2-4 mm; pileus pallid; on the ground in woods. North America. .... *L. americanus*

F. Stipe strongly eccentric, lateral, or even absent, usually very short; pileus cream color to alutaceous, expallent; on branches, mostly of *Abies alba*. Widely distributed .... *L. flabelliformis*

D. Stipe with more or less conspicuous longitudinal furrows; stipe either short or long but never lateral and never absent.

G. Stipe stuffed, then hollow, or solid; concolorous with the pileus (watery brown), or isabelline; taste acrid, or tardily

acrid; macrocystidia numerous; lamellae deeply decurrent or short-decurrent, white, then cremeous; stipe 7-32 mm long.

H. Furrows often very strongly developed and deep; pileus subhygrophanous. Europe and North Africa *L. omphalodes*

H. Furrows of the stipe fold like, short, not strong (stipe not or slightly wrinkled and scrobiculate); pileus hygrophanous. Eastern part of North America *L. umbilicatus*

G. Stipe stuffed, then hollow, brown to ferrugineous-brown, 30-40 mm long; macrocystidia not numerous; taste slightly acrid; lamellae sinuate-adnexed to sinuate decurrent. Alps, Caucasus, and Altai Mts. *L. bisus*

B. Stipe densely fasciculate; pileus often larger than 40 mm; odor of anise in most specimens. *L. cochleatus*

A. Stipe none.

I. Pileus usually glabrous or subglabrous but with strongly projecting rib-like veins, 30-150 mm broad, alutaceous to ferruginous; spores 2.5-3.8 μ broad. Temperate zone. *L. vulpinus*

I. Pileus entirely or only at the base covered with pallid or brown felt («ursinous»), at the margin sometimes pruinose or glabrous, ribbed-venose to subsmooth, pale brown, becoming more or less dark brown to bay, 10-70 mm broad; spores 2.4-2.5 μ broad. Temperate and tropical zones of both hemispheres. *L. ursinus*

30. MELANOLEUCA Pat.

Cat. rais. Pl. cell. Tunisie, p. 22. 1897.

Type species: Melanoleuca vulgaris Pat.

Syn.: Melaleuca Pat., *Hymen. Eur.* p. 96. 1887 (non Linné 1767).

Characters: Habit tricholomatoid, more rarely collybioid tricholomatoid or clitocyboid; pigment dusky or pale gray, fuscous, umber, etc., or absent; pileus glabrous, or pruinose, or innately fibrillose, most frequently perfectly glabrous, hygrophanous or non-hygrophanous, epicutis little differentiated, consisting of interwoven, repent, elongate hyphae that are not radially arranged; lamellae white, or cream colored, or grayish, usually close to crowded, emarginate to decurrent; spore print pure white to cream color (A to C of Crawshay); spores hyaline, subsmooth to (mostly) warty from a strongly amyloid exosporium (after the chemical removal of the exosporium the subangular shape of the spores is revealed when they are seen from one end) on a very slightly amyloid main wall, with a smooth

suprahilar disc (plage) on the inner side of the spores, the warts forming an ornamentation of the type III *b*, IV, V, or VI, the outline of the complete spores ellipsoid oblong, ellipsoid, more rarely short ellipsoid, the warts moderately high; basidia normal, rather short, 4-spored; leptocystidia or cystidioles (Pl. XXI, 4) usually present, very few species, and many individuals in certain species, devoid of cystidia; these cystidia rather characteristic, thin-walled, in one species thick-walled (transition to metuloids?), with an excretory function (often with thin crystals at the apex, or merely granulose at the tip and consequently arrow-shaped), subulate to fusoid; hymenophoral trama regular or almost so, with a slightly interwoven mediostratum, especially near the back of the lamellae; subhymenium cellular-subintermixed; stipe exelate, or much more rarely with an indistinct to distinct but rather incomplete annulus, usually central (very rarely eccentric), rather fibrous-fleshy in consistency and not truly cartilaginous or tough; context white, or, starting from the base of the stipe, becoming gray, brown, or almost black (from an intercellular-epicellular brown pigment characteristic for the genus), or colored so from the beginning; all hyphae without clamp connections. On the earth, in woods, and outside of the woods, often on manured pastures, in gardens, cold frames, greenhouses, also in prairies and steppes, even in semi-desert formations, also in the subalpine and alpine region and south to the tropical forests.

Development of the carpophores : Unknown.

Area : Cosmopolitan.

Limits : The delimitation of the genus *Melanoleuca* is not difficult in spite of the fact that what had been claimed as the main characters of the genus, viz. the cystidia and the ornamentation of the spores, are — though very frequent — by no means constant. In *Cantharellula*, it is perhaps the subgenus *Pseudoclitocybe* that comes closest to *Melanoleuca*, yet the perfectly smooth spores, the cyathiform pileus, and the absence of cystidia, also the shape of the spores and the production of HCN by the carpophores, taken together, should be sufficient to consider *Pseudoclitocybe* as generically different from *Melanoleuca*. The relation between *Cantharellula* and *Melanoleuca* is comparable to that existing between *Armillariella* and *Tricholoma*.

The delimitation from *Leucopaxillus* has been discussed under that latter genus.

State of knowledge : The genus has been studied by Singer (1935). The fact that most specific characters are macroscopic and require

accurate field notes, explains the absence of a monograph based on the world flora. It is fairly easy now to establish whether a dried specimen belongs in *Melanoleuca* but it is often difficult to point out its exact position in the intrageneric classification. The following conspectus of the sections and species is based mainly on the flora of Europe and Siberia, and partly also on the flora of New England, New York, and a few species from the Pacific Coast and Argentina-Paraguay. The number of species recognized here (i. e. definitively inserted in the classification) is 29.

Practical importance : As far as it is known now, the main practical importance of the genus *Melanoleuca* consists in the edibility of the carpophores of virtually all species. The most valuable edible mushrooms of this genus are *M. evenosa* and *M. alboflavida* (both, however, very little used).

SPECIES

Sect. 1. **ALBOFLAVIDAE** Sing. (1935 ut series, 1943). Pileus practically devoid of pigment, predominantly white, or bleaching to white, or ochraceous rather than grayish, or brownish; spore print (if pileus ochraceous) cream color, or, in other species, pure white; lamellae more often narrow than broad (narrow, in *Melanoleuca*, always means that the breadth of the lamellae is less than one tenth of the diameter of the pileus); spores either distinctly warty, or subsmooth.

Type species : M. alboflavida (Peck) Murr.

M. evenosa (Sacc.) Konrad (Tricholoma cnista ssp. evenosum Sacc.); *M. strictipes* (Karst. sensu Lundell) Sing. c. n. ad int. (Tricholoma, Karst. — perhaps identical with the preceding species, at least according to Lundell 1939 who also synonymizes Tricholoma pubifolium Romell,; *M. alboflavida* (Peck) Murr. (Collybia sedula Graff); *M. Kavinae* (Pilát & Vesely) Sing.; *M. Kalchbrenneri* Sing. (Agaricus dehiscens Kalchbr. non Viviani; Collybia, Sacc.; Melanoleuca, Sing.); *M. Balansae* (Speg.) Sing. (Clitocybe, Sacc.); probably also *M. candida* (Vel.) Sing.

Sect. 2. **HUMILES** Sing. (series, 1934; sect. 1943). Pileus well colored (gray, avellaneous-fuscous, fuscous, blackish), or soon becoming so; spore wall always distinctly warty from the well developed exosporium; stipe furfuraceous pubescent, or squamulose with black fibrils, or with an indistinct annulus; not entirely brown inside.

Type species : M. humilis (Pers. ex Fr.) Pat.

M. mirabilis (Bres.) Sing (Tricholoma, Bres.); *M. verrucipes* (Fr. apud Quél.) Sing [Armillaria, Quél.: Tricholoma, Bres.; Clitocybe puellula (Karst.) Karst.]; *M. humilis* (Pers. ex Fr.) Pat. (Tricholoma, Quél.).

Sect. 3. **OREINAE** Sing. (series, 1934; sect. 1943). Pileus and spores as in sect. 2; stipe usually merely pruinose at the apex, and if wholly pruinose, the interior of the stipe is entirely brown; small carpophores with white or gray stipe and white or gray lamellae; if the diameter of the pileus is larger than 30 mm and the stipe is not thin as in the genus *Collybia*, the lamellae are always white and narrow and the stipe is usually pallid. (Very large species do not enter this section).

Type species : M. oreina (Fr.) Kühner & Maire.

M. catalaunica Sing.; *M. oreina* (Fr.) Kühner & Maire (Tricholoma, Gillet); *M. graminicola* (Vel.) Kühner & Maire (Tricholoma, Vel.); *M. paedida* (Fr.) Kühner & Maire (Tricholoma, Quél.); *M. excissa* (Fr.) Sing. (Tricholoma, Quél.); *M. Spegazzinii* (Sacc. & D. Sacc.) Sing. (Tricholoma, Sacc. & D. Sacc.; Tricholoma humile Speg. non (Fr.) Quél.); probably also in this section: *M. subcinereiformis* Murr.; *M. Schumacheri* (Fr. sensu Killermann) Sing.; *M. testata* (Britz.) Sing.; *M. rasilis* (Fr. sensu Bres.) Sing.; also a species which may be partly *Tricholoma strictipes* Karst. (as such determined by the author once); perhaps *M. deserticola* (Speg.) Sing. (Tricholoma panaeolum var. deserticola Speg.).

Sect. 4. **VULGARES** Sing. (series, 1934; sect. 1943). Pileus, spores, and surface of the stipe as in the preceding section; however, small species, unless the context is brown to a large extent, with a diameter of the pileus of 30 mm or less, and collybioid stipe, are here excluded, and go to sect. *Oreinae;* the larger species have either colored stipe or broad (more than one tenth of the diameter of the pileus) lamellae.

Type species : M. vulgaris Pat.

M. grammopodia (Bull. ex. Fr.) Pat. (Tricholoma, Quél.); *M. cognata* (Fr.) Konr. & Maubl. (Tricholoma, Gillet) and its subspecies (geographic race) ssp. *altaica* Sing.; *M. crassotunicata* Sing.; *M. turrita* (Fr.) Sing. (Tricholoma, Sacc.); *M. polioleuca* (Fr.) Kühner & Maire (Melanoleuca vulgaris var. polioleuca Konr. & Maubl.); *M. brevipes* (Bull. ex Fr.) Pat. (Tricholoma, Quél.); *M. melaleuca* (Pers. ex Fr.) Murr. [Tricholoma, Quél.; Melaleuca vulgaris Pat.; Melanoleuca vul-

garis (Pat.) Pat.]; *M. planiceps* (Peck) Sing. (Tricholoma, Peck); *M. stridula* (Fr.) Sing. (Collybia, Quél.); *M. arcuata* (Fr.) Sing. (Tricholoma, Quél. sensu Ricken; Tricholoma Friesii Bres.); *M. Reai* Sing.; *M. luteolosperma* (Britz.) Sing. (Tricholoma, Sacc.); *M. subpulverulenta* Pers. ex Fr.) Sing. (Tricholoma, Karst.); *M. orientalis* (Pat.) Sing. (Collybia, Pat.); probably also in this section; *M. Earlei* (Murr.) Sing.; *M. praecox* Murr.; *M. montana* (Britz.) Sing.; *M. amica* (Fr. sensu Bres.) Sing.; *M. phaepodia* (Bull. ex Fr. sensu Bres., Sing.; *M. lixivia* (Fr. sensu) Maire.

Note: It may be possible to separate a section with cream colored spore print from the section *Vulgares* as outlined above. *M. Reai*, *M. luteolosperma* and others of this section are definitely cream spored (both these species occurring in both Europe and North America); other cream spored species (i. e. species now appearing in other sections than the *Vulgares*) may possibly later be combined with the section of cream-spored Melanoleucas. Such species are *M. alboflavida* (Peck) Murr. (non Sing. 1935), and at least one unpublished species from North America. However, a check on the exact color of the spore print of several species will be necessary before such a rearrangement could be contemplated. It is remarkable that, according to the author's experience, more cream-spored species occur in North America than in Europe.

KEY TO THE SPECIES

The most recent key cannot at present be essentially improved; cf. Singer in *Ann. Mycol.* 41: 50-57, 1943; the data in this key should be supplemented by additional data published by the author between the year 1942 and the present date.

GENERA INCOMPLETELY KNOWN

Dermoloma (Lange) stat. nov. ad. int. (*Tricholoma* subgenus *Dermoloma* Lange, *Dansk Bot. Ark.* 8: 12. 1933). Characters of *Tricholoma*; «cuticle of cap made up of subglobose-angular cells». Lange. The type species is *Tricholoma cuneifolium* (Fr.) Gill. sensu Lange. It appears that Lange's species is the same as that described under this name by Josserand, who indicates the spores as amyloid. If this indication is true — which there is no reason to doubt — *Dermoloma* can hardly any longer be considered as a subgenus of *Tricholoma*

unless the diagnosis of *Tricholoma* is changed. *T cuneifolium* is so little like a *Tricholoma* even in habit, that it does not seem to be an artificial solution to separate *Dermoloma* from *Tricholoma*. Among the *Leucopaxilleae* (where it would logically be looked for), there is no other genus with close affinities except perhaps *Cantharellula*, but even here, the differences separating it from *Dermoloma* are apparently on the generic level. A formal introduction of *Dermoloma* as an autonomous genus may be considered as premature by some mycologists, and the author hesitates to admit it without having seen authentic specimens.

Tribus RESUPINATEAE Sing.

Sydowia, **2**: 30, 1948.

Type genus *Resupinatus* Nees ex S. F. Gray.

Characters: Those of the family; hymenophore lamellate; basidia normal, i. e. not the *Lyophyllum* type; spores hyaline, smooth, nonamyloid, globose to short-ellipsoid, in some species also allantoid (curved) or ellipsoid-oblong with the inner side applanate, or ovoid; cheilocystidia usually present but not always conspicuous; metuloids (Pl. XXII, 2) often present on the sides of the lamellae; stipe rarely normally developed, often lateral and then the carpophores assuming a peculiar spathulate shape, or — most frequently — replaced by a pseudostipe which may be lateral (a mere prolongation of the rear side of the pileus, recognizable as a pseudostipe from below rather than from above), or else a discal pseudostipe; context soft and usually flexible when fresh, not becoming tough, consisting of nonamyloid tissue which is always at least partly gelatinized (Pl. XIX, 1), even in the hymenophoral trama of most species, the hyphae of the gelatinous layers thin, wavy, thin-walled, with clamp connections. Most frequently on decaying wood, more rarely on other vegetable matter in process of decomposition, or on diseased living tissue of *Cormophyta*.

KEY TO THE GENERA

A. Metuloids absent.	31. *Resupinatus*
A. Metuloids present.	32. *Hohenbuehelia*

31. RESUPINATUS Nees ex S. F. Gray

Nat. Arr. Brit. Pl. 1 : 617. 1821.

Type species : *R. applicatus* (Batsch ex Fr. sensu Kauffman) S. F. Gray.

Syn. : *Phyllotus* Karst., *Bidr. Finl. Nat. Folk* 32 : 14. 1879.
Scytinotopsis Sing., *Ann. Mycol.* 34 : 335. 1936.
Urospora Fayod, *Ann. Sc. Nat. Bot.* VII. 9 . 338. 1889 (descr. excl.) sensu Earle, *Bull. N. Y. Bot. Gard.* 5 . 418. 1909 ; sensu Singer, *Beih. Bot. Centralbl.* 56, B : 145. 1936.

Characters : Those of the tribus ; carpophores always resupinately attached, or with a pseudostipe ; metuloids none ; cheilocystidia often dendrophysoid. On wood and dead herbaceous plants, rarely on living plants.

Development of the carpophores : No recent studies available.

Area : Cosmopolitan.

Limits : This genus has originally been distinguished by Singer (1936), and the name Gray used was merely intended to characterize resupinate agarics, but has to be preferred for nomenclatorial reasons. However, it became necessary to restrict the diagnosis somewhat in order to exclude those species that do not have any gelatinized tissues. Some of these species have later been transferred to *Pleurocybella*, a genus then (1936) undescribed, others are still in need of more careful investigation (e. gr. *Pleurotus Langei* Pilát). The limits of the genus *Resupinatus* are fully determined by the diagnosis. The absence of metuloids has so far been found to be a character of sufficient stability and constancy to separate *Resupinatus* from *Hohenbuehelia* by a rather abrupt hiatus, and the character is one that is easy to verify. Notwithstanding the convenience of this diagnostic character, it cannot be doubted that *Resupinatus* and *Hohenbuehelia* are very closely related, and they have therefore been inserted in a common tribus.

State of knowledge : The recent monographs by Pilát (Europe) and Coker (North America) of the species involved, have helped to obtain a clearer picture of the systematics of these small, often overlooked and misdetermined agarics. From personal experience with fresh material, the author is fully familiar only with *R. applicatus* but there is no reason to reject the species indicated in the papers cited above on the basis of dried material or complete descriptive evidence

as supplied by these authors. This raises the number of species admitted in *Resupinatus* to seven.

Practical importance : Hardly any as far as present information is concerned.

SPECIES

R. applicatus (Batsch ex Fr. sensu Kauffman) S. F. Gray [Pleurotus, Quél.; Resupinatus atropellitus (Peck) Murr.]; *R. striatulus* (Fr.) Murr. (Pleurotus, Gillet); *R. silvanus* (Sacc.) Sing. (Agaricus silvanus Sacc.; Pleurotus alboniger Pat.); *R. unguicularis* (Fr.) Sing. (Pleurotus, Quél.); *R. cyphelliformis* (Berk.) Sing. [Agaricus, Berk.; Resupinatus campanulatus (Peck.) Murr.]; *R. Rhacodium* (Berk. & Curt.) Sing. (Agaricus, B. & C.); *R. chilensis* Sing.

KEY TO THE SPECIES[a]

A. Spores subglobose or globose
- B. Pileus nearly glabrous, very small, striate when fresh, sulcate when dry, said to occur on decorticated coniferous wood (Coker) . . . *R. striatulus*
- B. Pileus tomentose to strigose, not combining the above characters
  - C. Hairs of the disc dark brown to blackish brown . . . *R. Rhacodium*
  - C. Hairs of the disc not blackish but whitish to light brown . . . *R. applicatus*

A. Spores not globose
- D. Spores allantoid; lamellae white or whitish at maturity . . . *R. cyphelliformis*
- D. Spores not allantoid or slightly so; lamellae not whitish at maturity
  - E. Spores very broad: 6.3-7.5 × 4.2-6.3 μ; pileus very narrowly campanulate, up to 2 mm in diameter. Chile . . . *R. chilensis*
  - E. Spores more elongate; pileus broader; distribution wider
    - F. Pileus rugose; pseudostipe distinct . . . *R. unguicularis*
    - F. Pileus not distinctly rugose, not distinctly protracted into a pseudostipe. . . . *R. silvanus*

32. HOHENBUEHELIA Schulzer apud Schulzer, Kanitz & Knapp

Verh. zool. bot. Ges. Wien **16** : 45. 1866

Type species : *H. petaloides* (Bull. ex Fr.) Schulzer apud Schulzer, Kanitz & Knapp.

Syn. : *Pleurotus* sect. *Acanthocystis* Fayod, VII. **9** : 338. 1889
Sarcomyxa Karst., *Soc. Flor. faun. Fenn.* **18** : 62. 1891
Phyllotremella Lloyd, *Myc. Writ.* **6** : 1007. 1920.
Acanthocystis (Fayod) Kühner, *Contrib. Hymen.* (*Thèse*), p. 111. 1926

[a] This key is made up with the help of the author's own notes, and some data taken from Pilát's and Coker's keys.

Characters : Those of the tribus; metuloids present. These metuloids are very characteristic, deep-rooting, hyaline to stramineous bodies, the wall very thick and often distinctly formed by several layers, the tip or the entire outside usually incrusted by coarse crystals; the apex is obtuse or more often acute; these metuloids occur on the edges and on the sides of the lamellae (Pl. XXII, 2).

Development of the carpophores : Unknown.

Area : Cosmopolitan.

Limits : As for the delimitation against the genus *Resupinatus*, see under the latter genus. As for the separation of *Geopetalum*, see under that genus.

The metuloids are similar to those found in the *Lentineae*, viz. the group *Panus rudis*, and *Pleurotus floridanus*. *Hohenbuehelia* is distinguished from these genera by its fleshier, softer consistency its gelatinous layers in the trama, and the thinner, flexible hyphae of the mediostratum which is regular instead of irregular. Similar cystidia also occur in the genus *Campanella*. The latter differs from *Hohenbuehelia* in the shape of the hymenophore, and in the different manner of absorption of cresyl blue by the hymenal elements (see Singer, *Lloydia* **8** : 180. 1945).

State of knowledge : The papers cited above for *Resupinatus*, also contribute some interesting and valuable data on *Hohenbuehelia*. There are now at least 28 species the world over, and more may be found when a monographic treatment will be attempted in the future.

Practical importance : The Hohenbuehelias may occasionally be wood parasites of forest and fruit trees; some are reported to be edible, but their economical importance is small; at least one species is a possible source of antibiotic substances.

SPECIES

Subgenus I. **Serotinia** (Pilát) Sing. (*Pleurotus* sect. *Serotinia* Pilát 1935; *Acanthocystis sect. Serotini* Konr. & Maubl. 1938.) Metuloids obtuse, the walls remaining thin for a considerable time but finally becoming thick and complex.

Type species : H. serotina (Schrader ex Fr.) Sing.

H. serotina (Schrader ex Fr.) Sing. (*Pleurotus*, Quél.; *Acanthocystis*, Konr. & Maubl.).

Subgenus II. **Petaloides** (Konr. & Maubl.) Sing. (*Acanthocystis* sect. *Petaloides* Konr. & Maubl. 1938. Metuloids more or less acute, very soon becoming thick-walled.

Type species : *H. petaloides* (Bull. ex Fr.) Schulzer apud Schulzer, Kanitz & Knapp.

H. petaloides (Bull. ex Fr.) Schulzer apud Schulzer, Kanitz & Knapp (Pleurotus, Quél.; Acanthocystis, Kühner; Geopetalum, Pat.); *H. geogenius* (D. C. ex Fr.) Sing. (Pleurotus, Gillet; Acanthocystis, Kühner); *H. semiinfundibuliformis* (Karst.) Sing. (Pleurotus, Karst.); *H. alachuana* (Murr.) Sing. (Geopetalum, Murr.); *H. auriscalpium* (R. Maire) Sing. (Pleurotus, R. Maire, Acanthocystis, Konr. & Maubl.). (The preceding five species are perhaps too closely related to be specifically separated); also *H. angustata* (Berk.) Sing. [Panus, Berk.; Geopetalum, Murr.; Acanthocystis stratosa (Atk.) Sing]; *H. atrocaerulea* (Fr.) Sing. [Pleurotus, Quél.; Resupinatus, Murr.; Pleurotus, (Fr.) Quél.; Acanthocystis Sing.]; *H. grisea* (Peck) Sing. (Pleurotus, Peck; Resupinatus, Murr. if specifically different from the preceding species and *H. reniformis*); *H. myxotricha* (Lev.) Sing. (Pleurotus, Gillet; Acanthocystis, Konr. & Maubl.); *H. reniformis* (Fr.) Sing. (sensu Pilát.) [Agaricus, Fr.; Pleurotus applicatus (Batsch ex. Fr.) Quél. sensu Quelet, Karst., non al.; Pleurotus mustialiensis (Karst.) Karst.]; *H. subbarbata* (Berk. & Curt.) Sing. (Pleurotus, Sacc.; Resupinatus, Murr.).

Other species that can easily be identified as belonging in *Hohenbuehelia* judging from the published diagnoses are (in alphabetical order):

H. approximans (Peck) Sing.[77] (Pleurotus, Peck); *H. arata* (Pat. & Dem.) Sing. (Calathinus, Pat. & Dem.); *H. calceola* (Pat. & Dem.) Sing. (Calathinus, Pat. & Dem.) *H. cinereoalba* (Pat. & Dem.) Sing. (Pleurotus, Pat. & Dem.); *H. crustosa* (Coker nom. subnud.) Sing. (Pleurotus, Coker); *H. cubensis* (Murr.) Sing. (Geopetalum, Murr.); *H. elegans* (Coker nom. subnud.) Sing. (Pleurotus, Coker); *H. Harmandii* (Hariot & Pat.) Sing. (Pleurotus, Har. & Pat.; *Acanthocystis*, Sing.); *Lentinus hepatotrichus* Berk. (Acanthocystis, Sing.)[78]; *Pleurotus Hollandianus* Sumstine (Acanthocystis, Sing.)[79]; *H. mastrucata* (Fr.) Sing.; (Pleurotus, (Fr.) Sacc.; Acanthocystis, Konr. & Maubl.);

[77] Very close to *H. reniformis*, possibly too close.

[78] If the spores are ellipsoid as indicated, and the trama gelatinous, this belongs in *Hohenbuehelia*. A transfer is not made as the characters have not been checked on the type.

[79] This species is said to be identical with *P. mastrucatus* by Konrad & Maublanc and with *H. valesiaca* by Pilát. Until final settlement of the synonymy, a transfer of *P. Hollandianus* to *Hohenbuehelia* appears to be premature

H. nigra (Schwein.) Sing. (Agaricus, Schw.; Pleurotus, Sacc., Resupinatus, Murr.; Pleurotus Puttemansii Henn.; Acanthocystis, Sing.)[50]; *H. phalligera* (Mont.) Sing. (Agaricus, Mont.); *H. portegna* (Speg.) Sing.[51]; (Pleurotus, Speg.); *H. pruinosula* (Pat. & Dem.) Sing. (Calathinus, Pat. & Dem.); *H. sciadea* (Kalchbr. & McO.) Sing.; (Pleurotus Kalchbr. & McO.); *H. submastrucata* (Henn.) Sing. (Pleurotus, Henn.); *H. valesiaca* (Cesati apud Rab.) Sing. (Pleurotus, Sacc.).

Tribus PANELLEAE Sing.

Type genus : Panellus Karst.

Characters : Those of the family; habit of the carpophores pleurotoid; consistency more or less tough and reviving; usually partly gelatinous, more rarely not gelatinous; spores small to medium, cylindric, allantoid, or ellipsoid, smooth, amyloid. Mycelium lignicolous, rarely on grasses.

KEY TO THE GENERA

A. Hymenophore favoloid poroid; predominantly tropical genus
33. *Dictyopanus*

A. Hymenophore lamellate; predominantly temperate and boreal genus.
34. *Panellus*

33. DICTYOPANUS Pat.

Essai, p. 137. 1900.

Type species : Polyporus rhipidium Berk. [= *Dictyopanus pusillus* (Lév.) Sing.].

Characters : Habit of the carpophores pleurotoid (polyporoid); epicutis of the pileus and the edges of the pores with strongly diverticulate hyphae, sometimes showing a distinctly dichophysoid structure; hymenophore favoloid or poroid; trama of the pore walls gelatinous or non-gelatinous, and then irregularly interwoven; basidia small to medium-sized, 4-spored; cystidia none; cheilocystidia not strongly differentiated or replaced by dichophysate structures; basidioles fusoid; spores white in print, hyaline under the microscope, amyloid, smooth, small to medium (up to 7.8 μ), ellipsoid,

[50] *H. nigra* is very close to *H. reniformis* which differs in being substipitate.

[51] Said to be possibly identical with *H. atrocaerulea* (Pilát)

oblong ellipsoid, or ellipsoid cylindric; stipe lateral but often seemingly eccentric, comparatively short, often differentiated only below (and then hardly recognizable from above), or well individualized; trama mild or astringent, tough; on wood and on grasses.

Development of the carpophores : Unknown.

Area : Predominantly tropical but also rarely occurring in temperate North and South America.

Limits : This genus is reminiscent of certain species of *Favolaschia*. It differs, however, from that genus, in having non-gelatinous trama. *Dictyopanus Copelandii* resembles *Favolaschia* very closely but the author believes that — aside from phylogenetic speculation — there is no reason to assume that an immediate close affinity exists between *Dictyopanus* and *Favolaschia*.

State of knowledge : This genus has been monographically treated in a paper on the *Laschia* complex by R. Singer (*Lloydia*, **8** : 222. 1945), and all necessary data are now available on both species and varieties known.

Practical importance : Unknown.

SPECIES

D. Copelandii Pat.; *D. pusillus* (Lév.) Sing. (Gloeoporus, Lév.; Polyporus, Persoon ex Lloyd; Polyporus subpulverulentus Berk. & Curt.; Dictyopanus, Pat.; Laschia guaranitica Speg.) and its var. *rhipidium* (Berk.) Sing. (Polyporus rhipidium Berk.; Favolus, Sacc.; Gloeoporus, Speg.; Dictyopanus, Pat.).

KEY TO THE SPECIES

A key has been published in the author's paper (1945 *l. c.*

34. PANELLUS Karst.

Hattsv., Bidr. Finl. Nat. Folk **32** : XIV. 1879.

Type species : P. stypticus (Bull. ex Fr.) Karst.

Syn. : Scytinotus Karst., *loc. cit.*, p. XIV [type *S. ringens* (Fr.) Karst.]
Urospora Fayod, *Prodr.*, *Ann. Sc. Nat.* VII. **9** : 338. 1889 [e specie lectotypica : *Pleurotus mitis* (Pers. ex Fr.) Quél.].

Characters : Pileus rarely centrally (and then short) stipitate, more frequently eccentrically or laterally stipitate or subsessile; epicutis

consisting of filamentous hyphae which are more or less branched (sometimes almost at right angles, in other cases merely nodulose at places), or simple and undivided, sometimes spirally twisted; spore print white or whitish; spores hyaline, cylindric, smooth, usually small, more rarely medium sized, often more or less allantoid; basidia normal in all regards, 4-spored; cystidia none; cheilocystidia often present, not very prominent; stipe none, or lateral, or eccentric, often rising, without sharp limits, from an irregularly branched deep colored stroma, more frequently directly from the substratum (wood); context mild or with astringent taste, rather tough and very distinctly reviving when remoistened *in situ*; trama often with a distinct gelatinous layer; many hyphae with strongly thickened walls (some solid), all nonamyloid and with clamp connections.

Development of the carpophores: No recent studies available.

Area: Cosmopolitan, but most frequent in the temperate zone.

Limits: This genus can be distinguished from all other agarics with pleurotoid habit by its small, narrow, amyloid, smooth spores. Certain features, such as the frequently nodulose surface of some hyphae of *Panellus stypticus* are reminiscent of *Dictyopanus* which in fact does not differ from *Panellus* in any primary characters except for the configuration of the hymenophore. It is known that *Panellus stypticus* rarely occurs in a poroid form (which is induced by mechanical impediment); this form would be recognizable as a *Panellus* because of the absence of strongly gelatinized hymenophoral trama and narrow spores.

State of knowledge: All five species are well known.

Practical importance: *P. stypticus* often appears as a wound parasite which may, in combination with other pathogenic organisms contribute to the death of valuable trees.

SPECIES

P. stypticus (Bull. ex Fr.) Karst. [Panus, Fr.; Pleurotus, Pilát; Panus farinaceus (Schum. ex Fr.) Sacc.] with a luminescent and a non luminescent race; *P. mitis* (Pers. ex Fr.) Sing. (Pleurotus, Quél.); *P. rupicola* (Mass.) Sing. (Collybia, Mass.); *P. violaceofulvus* (Batsch ex Fr.) Sing. (Panus, Quél., Pleurotus, Pilát.); *P. ringens* (Fr.) Romagnesi (Lentinus, Fr.; Panus Delastrei Mont.; Lentinus michailowskoensis Henn.; Panus, Sacc.; Pleurotus, Pilát).

KEY TO THE SPECIES

A. Carpophores rising from a common stroma. India. *P. rupicola*

A. Carpophores rising from the substratum.

B. Taste styptic; nearly cosmopolitan (absent in the truly tropical belt). *P. stypticus*

B. Taste mild.

C. Pileus whitish; on coniferous wood; temperate zones. *P. mitis*

C. Pileus not whitish; on frondose and coniferous woods.

D. Spores 7-10 × 2-4 µ. *P. violaceofulvus*

D. Spores smaller. *P. ringens*

Tribus SCHIZOPHYLLEAE Henn.

in Engler & Prantl, *Nat. Pfl.-fam.*, 1 ** ; 221. 1898

Type genus : Schizophyllum Fr.

Characters : Habit of the carpophores pleurotoid; hymenophore very characteristic, lamellate but the sides of the lamellae splitting longitudinally in the hymenophoral trama and the halves rolling outwards, involute, more so in dry weather, less so in wet weather; spore print white to pinkish; spores hyaline, smooth, cylindric, or allantoid, or ellipsoid, nonamyloid; hymenophoral trama not bilateral nor inverse; basidia normal; context rather leathery to subcoriaceous, reviving and becoming toughish fleshy in wet weather, rather thin; hyphae thick walled; nonamyloid, with clamp connections; abhymenial hairs (free terminal members of the hyphae of the hymenophoral trama when reaching the space between the split open halves of the lamellae at the « edge ») usually somewhat differentiated. On wood, and other dead or living organic matter (even on citrus fruits, on *Fragraria*, etc.).

35. SCHIZOPHYLLUM Fr.

Syst. Mycol. 1 : 330. 1821.

Type species : Schizophyllum commune Fr.

Syn. : Apus Nees ex S. F. Gray, *Nat. Arr. Brit. Pl.* 1 : 617. 1821.
Schizonia Pers., *Mycol. Europ.* 3 : 14. 1828.
Rhipidium, *Wallr. Fl. Cr. Germ.* 2 : 742. 1833
Hyponevris Paulet ex Earle, *Bull. N. Y. Bot. Gard.* 5 : 411. 1909
Schizophyllus Fr. (1915) ex Murr., *North American Fl.* 9 (4) : 237. 1915

Characters : As in tribus.

Development of the carpophores : Gymnocarpous in *S. commune*.

Area : Cosmopolitan.

Limits : Schizophyllum is at present well delimited.

State of knowledge : Thanks to a monograph of the six species of the western hemisphere by D. H. Linder, the temperate and neo tropical species are well known.

Practical importance : Schizophyllum often damages agricultural crops, usually under circumstances otherwise unfavorable for the host plant. Truck, berries, etc. are attacked; fruit trees are also attacked mainly in wounds, and perhaps often as secondary infection. The author has observed *Schizophyllum radiatum* on recently harvested oranges in Florida, and *S. commune* on rhizomes of strawberries in Europe. Besides, all species of *Schizophyllum* are known to be rather active destroyers of wooden structures (railroad ties, telephone poles, etc.). The islanders in the Dutch East Indies and in Madagascar habitually chew carpophores of *Schizophyllum*.

SPECIES

Stirps **Commune** (Subhymenium well differentiated).

S. commune Fr.; *S. radiatum* (Swartz ex) Fr. (if not identical with *S. commune*); *S. brevilamellatum* Linder; *S. fasciatum* Pat.

Stirps **Umbrinum** (Subhymenium not differentiated).

S. umbrinum Berk.; *S. Leprieuri* Linder.

KEY TO THE SPECIES

The species named above are keyed out in Linder's paper (*Am. Journ. Bot.* **20** : 555. 1933).

Tribus LENTINEAE Fayod

Prodr., *Ann. Sci. Nat. Bot.* VII, **9** : 335. 1889 (ut Agaricacés, trib. Lentinés); Heim, *Treb. Mus. Cienc. Nat. Barcelona* **15** : 88. 1934; Imai, *Journ. Fac. Agric. Hokk. Imp. Univ.* **43** : 141. 1938.

Syn. : *Tricholomataceae*, subfam. *Pleurotoideae* Sing., *Ann. Mycol.* **34** : 334. 1936. *Pleuroteae* Kühn., *Contr.* p. 98. 1926 (ut Pleurotés); Imai, *l. c.* p. 92. 1938.

Type genus : Lentinus Fr.

Characters : Habit of the carpophores more or less pleurotoid, from stipitate in the center (but lignicolous and stipe curved or irregular, or inconstantly central) to sessile or pendulous-resupinate, but never effuso-resupinate; spores smooth, nonamyloid, thin walled to rather

thin walled, always elongate (length twice the breadth, or more), cylindric to cylindric suballantoid, or cylindric-ellipsoid oblong to fusoid, white, cream color, pale drab or pinkish drab, or rose color in print but sometimes expallent and becoming white in old prints; basidia normal (without carminophilous granulation); cystidia (mostly metuloids) sometimes present; cuticle of the pileus sometimes formed by dichophysoid structures; trama consisting of thick walled hyphae (at least some hyphae of the trama thick walled, i. e. with a wall more than 1 μ thick), nonamyloid, with clamp connections, very rarely without them; hymenophoral trama neither bilateral nor inverse; carbonaceous particles (green in KOH) never present. Most frequently on wood but also on other vegetable matter living as well as dead.

Note: In dry weather, the basidia are often all transformed into pseudoparaphyses with the shape of basidioles, yet remaining sterile indefinitely. In the hymenium, bunches of tramal hyphae are often found to project in the manner of the « pegs » of the genus *Coriolus (Polyporineae)*; part of the trama may be somewhat gelatinized, especially the surface of the thick walled hyphae but there are no conspicuous gelatinous layers, i. e. layers with thin walled wavy, thin hyphae which are truly imbedded in a mucus.

KEY TO THE GENERA

A. Lamellae deep colored, especially in dried material but also in fresh condition; black carbonaceous particles present in the tissue; they dissolve in alkali forming a greenish solution. (see *Anthracophyllum*, p. 205)

A. Hymenophore not deep colored in fresh condition, and hardly ever deep colored in well dried material; carbonaceous particles absent, tissue never green in alkali

B. Stipe absent, and veil present: hymenophore lamellate; spore print whitish to cream color. 36. *Tectella*

B. Not combining the characters indicated above.

C. Cuticle with dichophysoid structure, or hymenium with setae which are echinate (in the first case hymenophore lamellate, in the second case, hymenophore poroid or alveolate).

D. Cuticle with dichophysate stratum, hymenophore lamellate 42. *Asterotus*

D. Cuticle without dichophysate structure or hymenophore poroid or alveolate. (see *Asterochaete*, p. 283, and *Porodisculus*, p. 283)

C. Cuticle not dichophysate and setae absent.

E. Spore print pink when fresh, bleaching to white in the herbarium; spores small, allantoid; pileus covered with a hygrophanous tomentum. 37. *Phyllotopsis*

E. Spore print never pink; spores often small but usually not noticeably allantoid; pileus often tomentose but tomentum never hygrophanous

F. Hyphae of the trama persistently and permanently thin-walled, strongly and very irregularly interwoven; lamellae decurrent; stipe strongly developed, central or eccentric, with distinct veil. 38 *Pleurotus* (part)

F. Hyphae of the trama sometimes at first thin-walled but soon becoming thick walled, at least some of them; lamellae decurrent or not; stipe well developed, or not; veil present, or more often absent.

G. Hymenophoral trama completely irregular and subhymenium very inconspicuous, practically absent; metuloids present or absent; hymenophore not vein-like. 39. *Panus*

G. Hymenophoral trama completely irregular, and then subhymenium forming a well differentiated, broad layer, or trama regular to subregular; hymenophore lamellate, rarely venose.

H. Hymenophore lamellate, or, if venose, without metuloids.

I. Hymenophoral trama irregular to almost intermixed; subhymenium well differentiated and broad; pileus whitish or grayish to fuscous-umber, more rarely blue, green, red, yellow, or lilac; spore print often pale drab. 38. *Pleurotus* (part)

I. Hymenophoral trama not quite irregular but at least with a distinct axillar arrangement, at least many hyphae subparallel; subhymenium well developed, or not; pileus rusty to dull brown, melleous, tan color, or fulvous, more rarely without any pigment. 40. *Lentinus*

H. Hymenophore venose and provided with pseudoamyloid metuloids. 41. *Geopetalum*

36. TECTELLA Earle

Bull. N. Y. Bot. Gard. **5**: 433. 1909.

Type species: Panus operculatus B. & C. [= *Tectella patellaris* (Fr.) Murr.].

Characters: Pileus non-stipitate, resupinate to lateral; veil a pellicular veil that covers the lamellae in young specimens; spores up to

tely thin walls; basidia normal in every regard; cystidia none; trama regular or nearly so in the portion closer to the edge, less regular to irregular farther upwards, made up of thick walled to almost solid hyphae with nonamyloid reaction, with numerous clamp connections; spores appearing hyaline, but cream colored in a good print in some species; cystidia none at all, or sometimes some cheilocystidia present; pigment present, versicolor. On stumps and trunks.

Development of the carpophores: Probably hemiangiocarpous.

Area: Temperate zone.

Limits: The pellicular veil distinguishes this genus from the other *Lentineae*. The *Lentini* and *Pleuroti* that have no stipe are not distinctly veiled. The veiled *Lentini* have denticulate lacerate crenulate edges of the lamellae; the veiled *Pleuroti* have thin walled hyphae in the hymenophoral trama and softer context. *Phyllotopsis* differs in the absence of a veil, in the smaller, pink spores, and in a hygrophanous tomentum.

State of knowledge: Originally only one species was known. Now, a second one has been added (1943). A third one was tentatively placed in *Tectella* by the author but it was later transferred to *Pleurotus*.

Practical importance: Both species are wood destroyers. However, their comparative rarity prevents them from being seriously damaging in any region.

SPECIES

T. patellaris (Fr.) Murr. (Panus, Fr.; Panus operculatus Berk. & Curt.; Tectella, Earle); *T. calyptratus* (Lindbl. apud Fr.) Sing. (Agaricus, Fr.; Pleurotus, Sacc.).

37. PHYLLOTOPSIS (Gilbert & Donk apud Pilát) Sing.

Rev. Mycologie 1: 76. 1936.

Type species: *P. nidulans* (Pers. ex Fr.) Sing.

Syn.: *Pleurotus*, sect. *Phyllotopsis* Gilbert & Donk in litt. apud Pilát, in Kavina & Pilát, *Atlas Champ. Europe. Pleurotus* **14-15**: 169. 1935.

Pileus covered by a hygrophanous, dense tomentum (the tomentum regaining its color when moistened even in herbarium specimens), non stipitate, usually lateral; hymenophore lamellate; lamellae not white; spore print pink, bleaching to white in the herbarium; spores

hyaline, small, cylindric-allantoid, nonamyloid, subsmooth, thin-walled; basidia normal in every regard, 4 spored; cystidia none; if cheilocystidia are present, they are small, inconspicuous, filamentous, hyphae like; hymenophoral trama regular to subregular, consisting of subparallel to more or less interwoven hyphae with distinct axillar arrangement; subhymenium little differentiated, its elements smaller and shorter than those of the trama but not well separated from the latter; context rather thick, fleshy tough; hyphae nonamyloid, with numerous septa and clamp connections (Pl. XI, 4). On wood.

Development of the carpophores: No recent data available.

Area: Temperate zone.

Limits: This genus is small but well characterized by the color of the spore print, the shape of the spores and their size, the hygrophanous tomentum, and the absence of metuloids and a stipe.

State of knowledge: The type species is thoroughly known, at least as far as the data essential for its taxonomic position are concerned It is not quite certain whether a second species can be distinguished.

Practical importance: The type species is an active destroyer of wood, growing in hardwood as well as in coniferous wood.

SPECIES

P. nidulans (Pers. ex Fr.) Sing. (Pleurotus, Gillet; Crepidotus, Quél.; Panus, Pilát; Claudopus, Karst; Agaricus odorativus Britz.); perhaps *P. subnidulans* (Overholts) Sing. which however is said to have globulose spores.

38. **PLEUROTUS** (Fr.) Quél.

Champ. Jura Vosg., p. 62. 1872-73, em

Type species: *P. ostreatus* (Jacqu. ex Fr.) Quél.

Syn.: *Agaricus* trib. *Pleurotus* Fr., *Syst. Mycol.* **1**: 178. 1821.
Crepidopus Nees ex S. F. Gray, *Nat. Arr. Brit. Pl.* **1**: 616. 1821 (proposed for rejection).
Pleurotus Quél., *Enchir.*, p. 147. 1886 (homon. & synon.)
Dendrosarcus Paulet ex Kuntze, *Rev. Gen. Pl.* **32**: 462. 1889.
Lentodiopsis Bubák, *Hedwigia* **43**: 169. 1904 (type *L. albida* Bubák, *l. c.*).
Lentodiellum, Murr., *Mycologia* **7**: 216. 1915 (type *Panus concavus* Berk.)

Characters: Habit pleurotoid; pigment absent or almost absent, or present, and then grayish to fuscous-umber, more rarely blue,

green, red, yellow or lilac; hymenophore lamellate; hymenophoral trama completely irregular, consisting of thin walled or thick-walled hyphae (in the first case, veil present, and metuloids absent; in the second case, veil present or absent, metuloids present or absent); spore print pure white, or cream color, or very frequently pale drab (« tilleul buff », or paler — according to Ridgway's chart, or somewhat paler than « pale vinaceous buff »); spores hyaline, smooth, always cylindric, from rather small to large, with very thin to rather thin simple, nonamyloid walls; basidia normal in every regard; metuloids often present; cheilocystidia usually present; subhymenium (Pl. XXI, 1) always strongly developed, well differentiated and broad, differing from the irregular hymenophoral trama in the small size of the elements and often also in color (in dried material pale brownish instead of hyaline), often actually separating from the hymenophoral trama in alkaline media under slight pressure; stipe present, more rarely absent, at least as seen from above, and then the carpophores sessile; context fleshy to moderately tough and somewhat inclined to revive after remoistening; trama of the pileus nonamyloid, its hyphae with numerous clamp connections. On wood, more rarely on other plant tissues, on dead and on living hosts, very rarely on bones, or on the earth (probably seemingly so, actually on buried vegetable matter).

Development of the carpophores : Some species have been indicated as hemiangiocarpous (*P. dryinus, P. ostreatus* f. *cornucopioides*) but they might be pseudoangiocarpous as has been suspected by Kühner. The author has observed pseudoangiocarpous development in *P. hirtus*, and this might be generally the case in *Pleurotus* as should be demonstrated on primordia smaller than those used thus far.

Area : Cosmopolitan.

Limits : The traditional genera of this group, *Pleurotus, Lentinus,* and *Panus,* have been shown to be artificial, and during the last decades, several mycologists have contributed to their dismemberment, leaving a comparatively small nucleus of species within each of the old genera. However, little attention has been given to the delimitation of the three genera from each other. Two approaches were possible, both anatomical: either the presence or absence of metuloids could be made the major distinguishing character between *Panus* and *Pleurotus,* with *Lentinus* maintained according to the traditional macroscopical differences; or the structure of the sterile tissues of the hymenophore could be used for generic delimitation.

After checking on all the key species, and a large number of additional types, the author has decided in favor of the second principle. The metuloids do not seem to be quite constant. In some species of the section *Lentodiellum* which has been scattered among the *Pleuroti, Pani,* and *Lentini* by the authors of the past century, the species with metuloids pass almost imperceptively into species without them and these again are too close to the *Ostreatus*-group of *Pleurotus* to be separated from it generically. All these species have two characters in common: the irregular hymenophoral trama and the distinct subhymenium. The genus *Panus* is then separated on the basis of the absence of the subhymenium (or a very reduced, inconspicuous subhymenium may be present). In this case, we shall again find species with metuloids and without metuloids in the same genus, even in the same section. In fact, *P. crinitus* (*Lentinus crinitus* of the Friesian school) which the author has studied in abundance in the American tropics, is not materially different from the genus *Panus* in the narrower sense, except for the absence of the metuloids. Consequently what is left in the genus *Lentinus*, i. e. the groups *L. lepideus, L. adhaerens,* etc. can be separated from both *Panus* and *Pleurotus* by their subregular to regular hymenophoral trama. And again, in *Lentinus*, we find metuloids (here more elongate and less thick-walled) in some species while they are absent in the majority of the species. It appears, therefore, that the metuloids must be considered as a potential character in the *Lentineae*, or rather in the group *Pleurotus-Panus Lentinus*, but not as a generic character. When the species belonging to these three genera are sorted out according to their anatomical characters of the sterile tissues of the hymenophore, one will find that they are distributed along natural lines — each of the three emended genera now being perfectly homogeneous taxonomic groups, and the mycologist interested in the determination of the species is no longer compelled to go through all three genera in order to avoid missing the description of the species he is studying.

Under these circumstances, it seems to be well worthwhile to revise the position of the genus *Polyporus* in the light of this new arrangement. It will be remembered that both Kühner and Donk have indicated their conviction concerning the close affinity of *Polyporus* and *Lentinus*. Kühner has indeed substantiated this conviction by very good reasons which were summarized and augmented by Bondarzew & Singer — but only in regard to *Lentinus cyathiformis*. As for the other *Lentini* — and we may now add the *Pani*, and *Pleuroti*

— these latter authors said that only a more profound study of the tropical species (which represent the bulk of the species in these genera) will show which other species have to be considered as close to *Polyporus.*

The new classification of this group according to the structure of the trama and subhymenium makes it possible to see these relationships in a new light. Even a superficial examination of a number of species of the various sections of *Polyporus* shows quite clearly that all the structures of the sterile tissues of the hymenophore observed in the agarics (*Pleurotus, Panus* and *Lentinus*) are also present in *Polyporus.* This does not necessarily mean that *Polyporus* should also be divided into three autonomous genera but a striking parallelism of this kind is certainly indicative of affinity between these agarics on one side and the genus *Polyporus* on the other. If the corresponding groups are compared very carefully, it appears that the only reliable difference between them is the configuration of the hymenophore, a character whose domineering position in the taxonomy of the Higher *Basidiomycetes* has been questioned in recent papers (Singer 1945, Heim 1946). The genus *Pleurotus* has its poroid counterpart in *Polyporus dermoporus* Pers. (= *Favolus brasiliensis* Fr.) with which it also shares the comparatively fleshy consistency (even transparent in *P. dermoporus* and in some of the related species), the external aspect (so much so that it is often impossible to tell, without removing the carpophores from the substratum, whether the specimens belong to the agarics or to the polypores) and other important characters. One will therefore not be surprised to see that Patouillard as early as 1900 felt the affinity of these groups, and expressed it by putting *Favolus* in the agarics. A similar statement can be cited from one of Fries' papers. The genus *Panus* can be compared with the group around *Polyporus arcularius.* The reader will recall that this polypore is often picked up as an agaric, and only the examination of the configuration of the hymenophore reveals that it is a polypore. The similarity between this species and some of the species of *Panus* (in our sense) is striking, even as far as external appearance and the covering of the pileus and stipe is concerned. The genus *Lentinus,* at least the group *Cyathiformis,* may well be compared with *Polyporus squamosus,* as has been done by Kühner (1928).

The author does not go so far as to suggest the congenerity of the *Polyporus- dermoporus*-group with *Pleurotus.* However, it must be

understood that the only dependable difference between it and *Pleurotus* is in the shape of the hymenophore. This tends to make it difficult to maintain *Polyporus* in a group that is usually called *Polyporaceae* (« *Poria* », *Coriolus, Fomes*, etc.), and, instead of eliminating some species from the *Agaricales* by transferring them to *Polyporus*, we now face the necessity of absorbing taxonomically the entire genus *Polyporus* (one of the largest in the Higher *Basidiomycetes*) in the *Agaricales.* Whether this should be done within an additional tribus, *Polyporeae,* or, in an additional family *Polyporaceae* sensu stricto is not important. It is exclusively for practical (not theoretical) reasons that the author has decided to leave the polypores out of the present book since this subject is not suggested by the title of the book. The working methods, and traditional divisions have created a situation where the genus *Polyporus,* even in the narrower sense, is usually studied by another group of specialists than agaricologists, and concerns another circle of readers than those interested in the agarics and boletes as understood in the present sense. Furthermore, in transferring the genus *Polyporus* to the *Agaricales,* we would create a very embarrassing nomenclatorial situation. The genus *Polyporus* has always been considered as the type genus of the family *Polyporaceae.* Now, the *Polyporaceae* would become a family in the *Agaricales,* and the polypores remaining in the *Aphyllophorales* (the *Tyromyces*-group, the Porias, the *Daedaleopsis-Daedalea Lenzites-Gloeophyllum Coriolopsis Coriolus-Microporus*-group and also the *Fomes* group) would be without a valid family name. Besides, if the *Polyporaceae* would be considered as not different from the *Tricholomataceae,* this latter family, though predominantly lamellate, would become a synonym of the *Polyporaceae,* i. e. such genera as *Tricholoma, Collybia, Mycena,* etc., would become genera of the *Polyporaceae.*

The recognition of the affinity of the *Lentineae* and the genus *Polyporus* sensu stricto should not by any means lead to premature taxonomic arrangements. In the authors opinion, it is up to the polyporists to make a more detailed study of the species in question concentrating on the characters hitherto neglected and now emphasized in the *Agaricales,* and on the delimitation of the genus *Polyporus* sensu stricto from such genera as *Microporus,* i. e. genera which we consider to be typical *Aphyllophorales* showing a certain amount of superficial resemblance with *Polyporus.* The stipe in *Microporus* is essentially a pseudostipe, i. e. merely an elongation of the narrowed base

of the laterally attached carpophores of *Coriolus* and the like, whereas the stipe of *Polyporus* and *Pleurotus*, even though it may be somewhat reduced, is a true stipe. Also, the zonation of the *Microporus* (including «*Microporellus*») is a typically aphyllophoraceous feature, and the general analogy with agaricaceous genera comes to an abrupt end at this level. On the other hand, *Pseudofavolus* and *Mycobonia* are likely to be related to *Polyporus* sensu stricto.

As for the genus *Pleurotus*, it is sufficient to summarize the above in a few words :

1. A group of species [82] in the genus *Polyporus* sensu str. (= *Polyporellus* Karst.) has all essential characters of *Pleurotus* except the configuration of the hymenophore. This group, and therefore also all the other species of *Polyporus*, are related with the *Lentineae* (including *Pleurotus*) and will eventually be transferred to the *Agaricales*.

2. Other groups of *Polyporus* correspond to *Panus* and to *Lentinus* respectively. They contain the majority of the species of *Polyporus* [83].

State of knowledge : The genus *Pleurotus* is rather well known. However, the intraspecific taxonomy of certain stirpes (*Ostreatus*, *Sajor caju*, etc.) is still in need of revision, and the number of named

[82] *Polyporus dermoporus* Pers. (*Favolus brasiliensis* Fr.); *P. caespitosissimus* Sing. (*P. caespitosus* Lloyd non al.; *Favolus giganteus* Mont.); *P. subcaperatus* (Murr.) Sing. (*Hexagona*, Murr.; *Hexagona reniformis* Murr.; *Favolus caperatus* Pat.), etc.

[83] The author has studied the following species of *Polyporus* (in alphabetical order) : *P. admirabilis* Peck ; *P. alveolaris* D. C. ex Fr. (*Favolus europaeus* Fr. ; *F. ohiensis* B. & Mont.) ; *P. arcularius* (Batsch ex) Fr. (*P. alveolarius* Bosc ; *P. intermedius* Sing.) ; *P. brumalis* (Pers. ex) Fr. [*Polyporus polyporus* (Retz ex) Murr.] ; *P. caespitosissimus* Sing. (see footnote 82) ; *P. Conelli* Murr. (different from *P. tricholoma*) ; *P. Craterellus* Berk. & Curt. ; *P. dermoporus* Pers. (see footnote 82) ; *P. grammocephalus* Berk. ; *P. guyanensis* Mont. ; *P. Haudenii* Lohwag ; *P. hirtus* Quél. ; *P. hispidellus* Peck ; *P. infernalis* Berk. ; *P. intestinalis* Berk. ; *P. Kaernbachii* (Henn.) Sing. (*Favolus*, Henn.) ; *P. Leprieurii* Mont. and its variety var. *javanicus* Henn. ; *P. magnivarius* Lloyd ; *P. Masonii* (Murr.) Sing. (*Ceriomyces*, Murr.) ; *P. melanopus* Sw. ex) Fr. ; *P. moluccensis* (Mont.) Sing. (*Favolus*, Mont.) ; *P. fibrulosus* Lév. ; *P. radicatus* Schw. (*P. Morganii* Peck) ; *P. similis* Berk. & Curt. ; *P. subarcularius* Bond. ; *P. subcaperatus* (Murr.) Sing. (see footnote 82) ; *P. subradicatus* (Murr.) Sing. (*Scutiger*, Murr.) ; *P. squamosus* (Huds. ex) Fr. and species close to it considered as varieties by some authors (*P. Forquignonii* Quél. ; *P. coronatus* Rostk. ; *P. pennsylvanicus* Sumstine ; *P. fagicola* Murr., etc.) ; *P. tuberaster* (Jacq. ex) Fr. ; *P. tunetanus* (Pat.) Sacc. ; *P. tricholoma* Mont. (*P. stipitarius* Berk. & Curt.) ; *P. varius* (Pers. ex) Fr. [*P. elegans* (Bull. ex) Fr. ; *P. nummularius* (Bull. ex Fr.) Secr.], and probably *P. picipes* Fr.]

species now recognized (16) will almost certainly increase with the further exploration of the tropical flora. The solution of the difficulties met with by the taxonomist in the *Ostreatus*-group will probably necessitate a different approach, perhaps from the view point of sexuality rather than from pure morphology.

Practical importance: This genus contains some of the most valuable edible mushrooms of Eastern Asia, e. gr. *P. citrinopileatus*, *P. sajor-caju*. Some forms of *P. ostreatus* and *P. dryinus* may also be noted for occasional parasitism on living trees and for the wood-destroying properties of their mycelia. The sclerotium of *P. tuber-regium* serves the natives as food as well as for medical purposes.

SPECIES

Sect. 1. **LEPIOTARII** (Fr. ut *Agaricus*, Trib. *Pleurotus*, sect. *Excentrici* subsect. *Lepiotarii*) Pilát in Kavina & Pilát (1935) (gen. *Lentodiopsis* Bubák 1904). Trama consisting of thin-walled hyphae in the lamellae; veil present.

Type species: P. dryinus (Pers. ex Fr.) Quél.

P. dryinus (Pers. ex Fr.) Quél. [Armillaria, Schroeter; Armillariella Pat.; Pleurotus corticatus (Fr.) Quél.; P. pometi (Fr.) Quél.]; with var. *tephrotrichus* (Fr.) Sacc. [Pleurotus Albertinii (Fr.) Quél.; Lentodiopsis albida Bubák]; also *P. Rickii* Bres.

Sec. 2. **OSTREOMYCES** Pilát (1935) (subgen. *Concharia* Imai (1938, p.p.). Hyphae of the hymenophoral trama thick-walled; edge of the lamellae entire; pileus rather rarely without any pigment, more often with gray, fuscous umber, green, yellow, red, or blue to lilac pigment, cinnamon or rusty colors appearing only on drying in some specimens; context definitely fleshy even in age; veil none; metuloids none.

Type species: P. ostreatus (Jacq. ex Fr.) Quel.

P. ostreatus (Jacq. ex Fr.) Quél. [P. sapidus (Schulzer apud Kalchbr). Sacc.; P. cornucopiae (Paul. ex Pers.) Rolland; P. cornucopioides (Fr.) Gillet; Crepidopus subsapidus Murr.; P. parthenopeius (Comes) Sacc.; P. Yuccae R. Maire; P. Opuntiae (Dur. & Lév.) Sacc.; P. columbinus Quél. apud Bres.; P. salignus (Schrad. ex Fr.) Quél.; P. pulmonarius (Fr.) Quél.; P. convivarum Dunal & Delille apud Lagarde]; *P. laciniato-crenatus* (Speg.) Speg.; *P. citrinopileatus* Sing.; *P. pantoleucus* (Fr.) Gillet sensu Sacc. (Martianoff); *P. Phellodendri* (Sing.) Sing.

(Tectella, Sing. 1943); *P.* spec. [34]; *P. prometheus* (Berk. & Curt.) Sacc.; *P. importatus* Henn.; *P. Eryngii* (D.C. ex Fr.) Quél. [Clitocybe cardarella (Fr.) Sacc.; Pleurotus, Quel.; Pleurotus fuscus Ricken; Clitocybe tucala (Speg.) Sacc.].

Sect. 3. **LENTODIELLUM** (Murr.) Sing. (Genus *Lentodiellum* Murr.). Hymenophoral trama consisting of thick walled hyphae, at least in age; pileus pigment less or predominantly so, or else with a flush of cinnamon or buff or rusty color over part of the pileus; veil present or absent; sclerotium none.

Type species: Panus concavus Berk. sensu Murr. [= *Pleurotus hirtus* (Fr.) Sing.].

P. hirtus (Fr.) Sing. (Agaricus, Fr. non Secr.; Panus, Fr. 1838; Lentinus, Murr.; L. velleteus Berk. & Curt.; Panus infundibulum Berk. & Curt.; Panus concavus Berk., and several other synonyms whose type specimens have not been restudied); *P. subglaber* (Lloyd) Sing. (Lentinus Lloyd; Lentinus hirtiformis Murr. !); *P. sajor-caju* (Fr.) Sing. [Lentinus, Fr.; Lentinus leucochrous Lév. (p. p.!), and several other synonyms whose type specimens have not been studied thoroughly]; *P. levis* (Berk. & Curt.) Sing. (Panus, B. & C.; Lentinus, Murr.; Panus strigosus B. & C.); *P. floridanus* Sing.; perhaps also *P. Gemmelari* (Inz.) Sacc. (P. Cavarae Bres.).

Sect. 4. **TUBER-REGIUM** Sing. Somewhat more colored than the species of the preceding section, and generally like the latter but with a conspicuous *Pachyma*-sclerotium.

Type species: P. tuber regium (Fr.) Sing.

P. tuber regium (Fr.) Sing. [Lentinus tuber-regium (Fr.) Fr.]; *Lentinus Woermannii* Cohn & Henn. is probably the West African form of this species.

KEY TO THE SPECIES

A Tramal hyphae thin-walled (all walls thinner than 1 μ even in fully mature carpophores; veil present. *P. dryinus*

A Tramal hyphae in mature specimens thick-walled, or at least a majority of them with walls thicker than 1 μ.

B Pileus white or with a slight cinnamon or buff or rusty shade on part of the carpophores, or with colored squamules, with or without a sclerotium

C Pileus with erect, soft hairs in young as well as in old specimens; temperate species in North America. *P. levis*

[34] This species was sent to the author by Rick from Brazil under the name of *Paxillus miniatus* with which it does not agree except for the red color.

C. Pileus not so strikingly covered with soft erect hairs, at least not in fully mature specimens, or not all over; tropical species.

D. A conspicuous sclerotium (or pseudosclerotium) present.
P. tuber-regium, *P. Woermannii*

D. Sclerotium none.

E. Metuloids none, or rare and inconstant, or poorly developed.

F. Pileus glabrous in youth (or slightly villous near the point or line of attachment).

G. Spores 6.5-11 × 2.5 μ, or larger.
(see *P. ostreatus* and *P. Eryngii*)

G. Spores smaller: 5-6 (8) × 2-3.3 μ.

H. Luminescent species in Eastern Asia.
P. prometheus

H. Non luminescent species in Northern Europe and Siberia. *P. pantoleucus*

F. Pileus not glabrous in youth.

I. Spores 5.3-9 × 2-3.3 μ.

J. Pileus and stipe in fresh condition distinctly flocculose-scaly from the veil, later glabrescent, besides somewhat velutinous or vellereous on the margin when young. Eastern Asia.
P. sajur-caju

J. Pileus and stipe never flocculose-scaly or very indistinctly so, however, distinctly vellereous-velvety all over when young, only very old specimens glabrescent. American subtropics and tropics. *P. hirtus*

I. Spores larger. *P. subglaber*

E. Metuloids very numerous, constant, and typical. Florida.
P. floridanus

B. Pileus not colored as above; sclerotium none.

K. Lamellae red or pink or orange-scarlet.

L. South American species; spores 7.2-7.5 × 3.3-3.8 μ. (see *P. spec.*)

L. East Asiatic species; spores 10-11 × 3.3-4 μ. *P. Phellodendri*

K. Lamellae not red.

M. Pileus appressedly squamulose all over. *P. importatus*

M. Pileus glabrous (or finely villous).

N. Pileus bright yellow. *P. citrinopileatus*

N. Pileus not bright yellow, or occasionally becoming partly yellow on drying.

O. On wood and succulent tissue, not on *Umbelliferae*.
P. ostreatus

O. On *Umbelliferae*. *P. Eryngii*

39. PANUS Fr.

Epicrisis, p. 396. 1838, em.

Type species: *P. conchatus* (Bull. ex Fr.) Fr.

Syn.: *Pleuropus* (Pers. ex) S. F. Gray, *Nat. arr. Brit. Pl.* 1: 615. 1821 (proposed for rejection).
Scleroma Fr., *Epicr.*, p. 387. 1838 (lectotype proposed: *Lentinus velutinus* Fr.).
Pocillaria B. Browne ex O. Kuntze, *Rev. Gen. Pl.* 2: 865. 1891.
Lentodium Morgan, *Journ. Cincinnati Soc. Nat. Hist.* 18: 36. 1895.
Lentinopanus (Pilát ut sect. *Pleuroti*) Pilát, *Ann. Mycol.* 39: 73. 1941 [1942].

Characters: Habit pleurotoid, but often with central stipe, and then differing from the genera with non-pleurotoid habit in being very tough and reviving, and growing on wood; pigment present but usually not bright colored except in fresh specimens of section *Conchati* where it is lilac; hymenophore lamellate; lamellae decurrent (if there is a stipe); hymenophoral trama completely irregular, (Pl. XXI, 5), consisting of thick-walled hyphae; spore print white; spores hyaline, smooth, nonamyloid, always cylindric, from rather small to medium (mostly not more than 8 μ long), with very thin to rather thin simple wall; basidia normal in every regard; metuloids often present, and then usually obtuse at the apex and rather short, with extremely thick walls, mostly moderately numerous; subhymenium very little developed, hardly noticeable (Pl. XXI, 5); edge of the lamellae lacerate-denticulate-crenulate, or entire; stipe present, more rarely absent and then carpophores sessile; veil usually none [55]; context very tough and reviving on remoistening of a nonamyloid trama; clamp connections numerous. On wood.

Development of the carpophores: Gymnocarpous in *Panus conchatus* according to Kühner, probably almost (pseudo?) angiocarpous in some hairy species where part of the hymenia of the primordia is hidden under the involute margin; pseudo-angiocarpous in *P. tigrinus*.

Area: Pantropical and cosmopolitan species predominant.

Limits: The delimitation of this genus against *Pleurotus* and *Lentinus* is discussed under the correspondent paragraphs in those genera.

Morgan and Murrill have seen fit to recognize a separate genus for an abnormal form of *Panus tigrinus*. Since the carpophores which

[55] In an undetermined species, known to the author from a single collection from Argentina, there was a distinct floccose veil as in some *Pleuroti*.

the author has studied are always sterile, and the configuration of the hymenophore is one of the gastroid type, i. e. abnormal in the *Agaricales*, it appears to be better to refer to these forms as the *Lentodium* forms of *Panus tigrinus* rather than to a separate species or genus. The *Lentodium* forms have been found in North America (New England west to Illinois), not in other parts of the enormous area of *P. tigrinus*. This, however, is not unusual for a mutation of this kind.

The genus *Scleroma* has been validly published by Fries in spite of the fact that it was ineptly described (because Fries had never seen fresh specimens) and no species were ever transferred to it. *Lentinus velutinus* is the only well known species that enters the group of species indicated by Fries as belonging to *Scleroma*, and it is therefore considered as a convenient lectotype. Since *Lentinus velutinus* is a *Panus*, *Scleroma* becomes a synonym of *Panus*.

State of knowledge: Our present knowledge of the species of *Panus* is very satisfactory. There are only about twenty species in existence. The remaining species of *Panus* and *Lentinus* (as far as they do not go into other genera than *Panus*) are mostly synonyms of the species indicated below. A future monograph of the genus will have to clear up the synonymy of this genus, especially of such species as *P. crinitus*, *P. siparius* and *P. tigrinus*. At present, the author indicates only eight species.

Practical importance: All species are very active wood destroyers. *P. rudis* is important in the preparation of *airan* (a fermented milk product) in the Caucasus.

SPECIES

Sect. 1. PLEUROTI (Sacc. 1887 ut sect. generis *Lentini*) Sing. Metuloids none; pileus glabrous; tramal hyphae rather thin, the majority almost solid or with very narrow lumen; edge of the lamellae denticulate; stipe eccentric, lateral, or absent; if the stipe is present, there is usually a deep red zone at the base (corresponding) to the black zone of « *Melanopus* » in *Polyporus*).

Type species: *Lentinus suavissimus* Fr.

P. suavissimus (Fr.) Sing. (Lentinus, Fr.; Lentinus haematopus Berk.; Panellus, Murr.; Lentinus anisatus Henn.).

Note: This section corresponds to *Polyporus guyanensis* and related species.

Sect. 2. CRINITI (Sacc.) Sing. (*Lentinus,* sect. *Mesopodes* subsect. *Criniti* Sacc. 1887). Metuloids few or none; pileus often pilose or with pilose-fibrous squamules, often striate; hyphae of the hymenophoral trama filamentous, moderately thin, not many almost solid; edge of the lamellae either permanently entire, or becoming lacerate-serrulate or almost denticulate in age; stipe central or eccentric.

Type species: Lentinus crinitus (L. ex Fr.) Fr.

P. tigrinus (Bull. ex Fr.) Sing. (Lentinus, Fr.); *P. Schnyderi* (Speg.) Sing. (Lentinus, Speg.); *P. crinitus* (L. ex Fr.) Sing. (Lentinus, Fr.; L. Schomburgii Berk.; L. tener Klotzsch ex Fr. sensu Berk. & Curt.; L. stuppeus Klotzsch ex Fr. sensu Berk. & Curt.; L. Wrightii Berk. & Curt.; L. subcervinus Berk. & Curt.; L. rigidulus Berk. & Curt.; L. pyramidatus Berk. & Curt.; L. nicaraguensis Berk. & Curt.; L. villosus Fr. sensu Berk. & Curt.; L. nepalensis Berk. sensu Berk. & Curt.; probably several more synonyms whose type specimens have not been restudied); *P. echinopus* (Lév.); *P. siparius* (Berk. & Curt.) Sing. (Lentinus, Berk. & Curt.; Lentinus velutinus Fr.; L. blepharodes Berk. & Curt.; probably several more species whose type specimens have not been restudied).

Note: This section corresponds to *Polyporus arcularius* and related species.

Sect. 3. CONCHATI Fr. (1868) (Genus *Lentinopanus* Pilát). Obtuse metuloids usually present, rather scattered, with very thick walls and little (if at all) projecting; pileus hirsute, in the center sometimes squamulose at the same time, or entirely glabrous (but then metuloids constant) and smooth; pigment some kind of pale brownish to almost cinnamon, and often flushed with a beautiful lilac when quite fresh (not regained when revived); edge of the lamellae not denticulate, always entire; hymenophoral trama as in section 2.

Type species: P. conchatus (Bull. ex Fr.) Fr.

P. conchatus (Bull. ex Fr.) Fr. [Lentinus, Schroter non Mont.; Panus torulosus Fr.; Lentinus carneotomentosus (Batsch ex) Schröter]; *P. rudis* Fr. [Lentinus strigosus (Schw.) Fr. non Panus strigosus Berk. & Curt.; Agaricus hirtus Secr. non Fr.; Lentinus Lecomtei Fr.; Panus guaraniticus Speg.; Lentinus Martianoffianus Kalchbr.] with f. *Sainsonii* (Lév.) Malkowsky [Panus Sainsonii (Lév.) Heufler], var. *subrudis* (Sing.) Sing. (Panus subrudis Sing. 1936), and var. *strigellus* (Berk. & Curt.) Sing (Lentinus strigellus, B. & C.; Panus, Sing. 1943)

KEY TO THE SPECIES

A. Pileus glabrous.
  B. Cystidia none; lamellae denticulate when mature. *P. suavissimus*
  B. Metuloids present; lamellae entire when mature. *P. conchatus*
A. Pileus hairy or scaly.
  C. Stipe finely velvety, pseudosclerotia present; cystidia rarely present; pantropical species. *P. tuparius*
  C. Stipe not velvety (either with erect irregular hairs, or rather scaly than velvety, or hirsute strigose); pseudosclerotia none.
    D. Metuloids absent, or very scattered and often atypical
      E. Pileus mostly scaly, never hairy. *P. tigrinus*
      E. Pileus hairy.
        F. Asiatic species. *P. echinopus*
        F. American species.
          G. Center and margin pilose; hairs of margin ± colored. *P. crinitus*
          G. Center squamulose, marginal hairs pure white. *P. Schnyderi.*
    D. Metuloids constantly present, rarely very scattered and somewhat inconstant, and then pileus hirsute. *P. rudis*

40. LENTINUS Fr.

Sisp. Agri Feme. 3: 57. 1825, em.

Type species: Lentinus lepideus Fr.

Syn.: Lentinula Earle, *Bull. N. Y. Bot. Gard.* 5: 416. 1909

Characters: Habit as in the preceding genus; pigment present, but often only in the scales of the pileus, and/or appearing in the carpophores in age on drying (yellow), tan color, cinnamon, fulvous, chestnut, ochraceous, etc.; hymenophore usually lamellate, exceptionally irpicoid or with conspicuous anastomoses between the lamellae adnate or decurrent, edge of the lamellae denticulate, lacerate, crenulate, or serrulate, at least in age; hymenophoral trama not completely irregular but regular to subregular in young specimens, its hyphae subparallel or interwoven but always distinctly axillarly arranged, thin walled at first in many species, but eventually at least many of them becoming thick-walled (wall 1 μ or more thick); basidia normal in every regard; spore print white; spores hyaline, smooth, nonamyloid, ellipsoid oblong to cylindric, or fusoid, from small to large, with very thin to rather thin simple wall; metuloids absent, or present, and then with moderately thick walls, with obtuse apices.

and considerably projecting in most cases; subhymenium either very poorly developed, or more or less differentiated; stipe always present, central to strongly eccentric; veil sometimes present; context fleshy, soon becoming rather tough, reviving when remoistened in situ; hyphae of the trama at least partly thick walled, nonamyloid, with clamp connections. On woody substrata, perhaps also on grass roots, often on buried wood, or on charcoal.

Development of the carpophores : Pseudoangiocarpous in some species, probably gymnocarpous in others.

Area : Cosmopolitan (but none of the species as such is cosmopolitan); several species are tropical or subtropical, the rest subtropical and temperate.

Limits : It has formerly been thought that *Panus tigrinus* is very closely related to *Lentinus lepideus.* This is not the case. The sterile tissue of the lamellae has a different structure in these species, and the affinities of each of these species are with quite different groups. *P. tigrinus* is so similar to *P. crinitus* that it is often almost impossible to tell the two species apart when they grow together in the American subtropics because *P. crinitus* sometimes becomes glabrous in age under the influence of heavy rains. etc. *L. lepideus,* on the other hand, does not resemble any species of *Panus.* It is closely related to such species as *L. adhaerens,* all species with comparatively thin walled hyphae in youth, rather thick or rather soft when fresh, and often used as edible mushrooms. All these species have the hymenophoral trama more regular than the species of *Panus.* If all the species with completely irregular hymenophoral trama and undeveloped subhymenium are excluded from *Lentinus,* a group of sections is left that, together, may well be admitted as a natural genus, viz. *Lentinus* in a narrower sense. In this sense, the *Lentini* do not include any species with hairy pileus, or with very thin, leathery pileus, or with astipitate carpophores, or with sclerotium.

In the future, on the basis of more data on the development of the carpophores of the species of *Lentinus* em., it will be possible to decide whether or not *L. cyathiformis* should be left within the genus *Lentinus.* It is not impossible that this species will eventually be removed from *Lentinus* on the basis of the development of the hymenophore (which is venose as in *Cantharellus* in specimens that are not fully developed).

State of knowledge : The species of *Lentinus* in the present sense is rather complete except for development studies. It would be parti-

cularly interesting to extend these studies to all species of *Lentinus*. The author has admitted eight species. The remaining available types were not in a condition to be studied anatomically, or else they turned out to be probable synonyms of the species indicated. Other species must be transferred to one of the other genera of the *Tricholomataceae*. Several species are perhaps still undescribed in spite of the large number of names available in Saccardo.

Practical importance: Several species of *Lentinus* have a considerable economic value, e. gr. *L. edodes*, a species widely used in oriental cooking, and sold in fresh, dried, and canned condition in China, Japan, and everywhere where Chinese and Japanese live, even all through the Malays and the Philippines. This species is grown commercially in China and Japan; in Japan, the methods are now based on scientific results, and the yield has subsequently increased; in China, the growing is still primitive. It is done by watering old trunks of *Pasania* and oak in a neighborhood where *L. edodes* grows wild. The Japanese growers now rely on pure cultures. The fungus is known as *shiitake* (Japanese). Another edible fungus of this genus is *L. cubensis*.

L. Kauffmanii appears to be one of the two most dangerous parasites on living conifers in British Columbia, especially on *Picea sitchensis* and other commercially important (*P. sitchensis* is used for aircraft production) lumber trees. It causes brown pocket rot.

Several species of *Lentinus* inflict considerable damage to wooden structures and building material. The most important wood-destroyer (though practically limited to coniferous wood) is *L. lepideus*. It is often very common on railway ties, on bridges, even on wooden houses, on all kinds of wood used in mines.

SPECIES

Sect. 1. **VARIABILES** Sing. (1948). Lamellae at first obtuse and venose, gradually broadening and reaching full size only at or after full maturity, the broadening taking place by the way of a growth line along the edge of the lamellae which consists of actively dividing hyphal elements which are often similar to cheilocystidia; hymenophoral trama subirregular in the upper part, at least in the mature specimens, subregular in the portion near the edge, rather loosely arranged, consisting of filamentous, rather thick walled hyphae; the subhymenium moderately well developed, comparatively loose, not

thick; metuloids none; clamp connections present; veil none; margin not sulcate.

L. cyathiformis (Schaeff., ex Fr.) Bres. (L. variabilis Schulzer apud Quél.; L. degener Kalchbr. apud Fr.).

Sect. 2. **SQUAMOSI** Fr. (1863) (*Mesopodes* subsect. *Lepidei* Fr. 1874) Lamellae not venose for a long time; hymenophoral trama regular, consisting of moderately thick-walled hyphae which are subinterwoven in the central portion of the trama (mediostratum) and more strictly parallel near the subhymenium or the hymenium; subhymenium either negligible or well developed, consisting of thin, small hyphae, ramose, with crowded septa; metuloids present or absent; veil present or absent; clamp connections present; margin not sulcate.

Type species: L. lepideus Fr.

L. lepideus Fr.; *L. spretus* Peck [44]; *L. cubensis* Berk. & Curt. [L. proximus Berk. & Curt.; Lentinula detonsa (Fr.) Murr. sensu Murrill an Lentinus detonsus Fr.?]; *L. Kauffmanii* A. H. Smith (if specifically different from the following species); *L. adhaerens* (A. & S. ex Fr.) Fr.; *L. edodes* (Berk.) Sing. (Agaricus Berk.; Armillaria, Sacc.; Cortinellus S. Ito & Imai; Collybia Shiitake Schröt.; Tricholoma, Ramsbottom; Pleurotus Bretschneideri Kalchbr. sensu Torrend; Lentinus tonkinensis Pat.).

Sect. 3. **FULVIDI** Sing. (1943). Lamellae not venose for a long time; hymenophoral trama regular or subregular in young specimens, at least near the edge, consisting of thick walled and some thin walled filamentous hyphae and some connective hyphae; subhymenium little developed; metuloids present or absent; clamp connections absent or few in *L. sulcatus*; veil present, but little developed; margin of the pileus deeply sulcate; pigment of the cuticle of the pileus abundant, yellow (fulvous macroscopically).

Type species: L. fulvidus (Bres.) Pilát.

L. fulvidus (Bres.) Pilát (Panus, Bres.); *L. sulcatus* Berk.

KEY TO THE SPECIES

A. Metuloids present, projecting, subcylindric
  B. Spores small (smaller than 8 µ long).
    C. Pileus pulverulent-flocculose-sticky ... *L. adhaerens*
    C. Pileus not so. ... *L. Kauffmanii*
  B. Spores much larger. ... *L. fulvidus*

[44] *L. spretus* is probably a subspecies of *L. lepideus*

A. Metaloids absent.

D. Margin of the pileus strongly and deeply sulcate ; spores and basidia very large. American species. *L. sulcatus*

D. Margin of the pileus not strongly sulcate ; spores and basidia small to medium size.

E. Spores medium sized ; if the lamellae are non-decurrent, the odor is very strongly aromatic ; if the mycelium grows on frondose wood, the lamellae are usually venose in young specimens. Species distributed predominantly in the temperate zones in both hemispheres.

F. Lamellae initially venose, later broad and decurrent; veil none; on frondose wood in the temperate zone of the eastern hemisphere. *L. cyathiformis*

F. Lamellae initially not venose, decurrent, or not decurrent ; veil present (though sometimes poorly developed, especially in the form with decurrent lamellae) , on coniferous wood, rarely on *Populus*.

G. Pileus usually umbonate, squamulose, rather thin to thick; lamellae decidedly decurrent ; stipe indistinctly veiled ; odor weak ; American species. *L. spretus*

G. Pileus obtuse, squamose in most specimens, rarely almost naked ; lamellae sinuate-adnate-subdecurrent to adnato-decurrent , stipe usually distinctly veiled ; odor very strong aromatic. Temperate zones. *L. lepideus*

E. Spores small , on frondose wood in East Asia and in subtropical and tropical America ; odor none ; lamellae never decurrent.

H. Pileus and stipe predominantly white, at least in youth, with small squamules in many specimens American species. *L. cubensis*

H. Pileus entirely brown in youth, later with large subappressed scales, or areolate from cracking Asiatic species ". *L. edodes*

41. GEOPETALUM Pat.

Hymen. Europe, p. 127. 1887.

Type species . *Cantharellus carbonarius* A. & S. ex Fr.

Characters: Habit clitocyboid, but at times somewhat eccentrically stipitate and pileus strongly depressed ; cuticle consisting of hyphae which form indistinct floccons consisting of a trichodermium but becoming very strongly applanate at least in their outermost layer and consequently appearing dense, pigmented with a stramineous to brown intracellular pigment but the hyphal walls also pigmented (same color), smooth ; hymenophore lamellate-venose ; lamellae very narrow and obtuse and usually strongly forked, decurrent, arcuate

" There is also a South American colored species in this group, *L. Sayana* Sing. ined.

or straight descendant, dull cremeous to dull cinereous in age; spore print color not known, supposedly white; spores hyaline, smooth, cylindric, cylindric ellipsoid oblong to recurved (i. e. sausage-shaped with the inner side convex and the outer side concave), asymmetric, nonamyloid, with rather thin, simple wall; basidia usually 4 spored, some 1-, 2, or 3-spored, narrower than the length of the spores and 4 4.5 times as long as the length of the spores; metuloids comparable with those of *Pleurotus* and *Hohenbuchelia*, pseudoamyloid, with crystalline incrustation in the free portion, acute or subacute at the apex, strongly metachromatic (pinkish lilaceous on blue to violet background provided by the basidia); subhymenium present, slightly colored (the trama being hyaline), consisting of very small and short elements; structure of the hymenophoral trama not quite distinct because of the age of the material studied and the venosity of the hymenophore, but apparently subintermixed, many of the hyphae thick walled; stipe often subradicant, without veil, central or eccentric, more or less vertical, solid; context fleshy tough, not soft nor watery, consisting of thin- to thick walled non amyloid hyphae with clamp connections, without gelatinous layer. On charcoal.

Development of the carpophores: Not known (probably gymnocarpous).

Area: Europe.

Limits: The somewhat tough, dry consistency, the presence of typical pseudoamyloid metuloids, the vein-like character of the hymenophore, and the absence of a gelatinous layer in the context are sufficiently important characters to separate *Geopetalum* generically from the genera of the *Resupinateae* as well as from those of the *Lentineae*. The author has transferred this genus to the latter tribus because of the absence of a gelatinous layer, and the elongate spores tending to be recurved. The presence of metuloids alone would not be sufficient reason to consider this genus as related with or identical with *Hohenbuchelia*, inasmuch as some species of *Pleurotus* have very similar metuloids. The venose character of the hymenophore can be compared with that of *Lentinus cyathiformis* in immature specimens whereas in *Geopetalum*, at least in *G. carbonarium*, the hymenophore never becomes truly lamellate. It is always difficult to delimit and define a monotypic genus. At present, *Geopetalum* seems to be extremely well separated.

State of knowledge: The only species referable to this genus is rather well known, yet there are certain minor items that are in need

of further observation (development of the carpophores, characters of the fresh specimens such as the spore print in thick layer observed before dehydration).

Practical importance : None.

SPECIES

G. carbonarium (A. & S. ex Fr.) Pat. [Merulius carbonarius A. & S.; Cantharellus carbonarius (A. & S. ex Fr.) Pers. ; Cantharellus umbonatus var. carbonarius (A. & S. ex) Fr.; Cantharellus anthracophilus Lév. ; Cantharellus radicosus Berk. & Br.].

42. ASTEROTUS Sing.

Mycologia **35** : 161. 1943.

Type species : *Panus dealbatus* Berk.

Characters : Habit pleurotoid; pileus flabelliform ; surface layer of the pileus formed by a dichophysate stratum (hyphae branching with short, crowded side branchlets at right angles in all directions), often reminding one of the so called *Asterostromella* structure, the terminal branchlets often star shaped when seen from above (Pl. XVI, 2); hymenophore lamellate ; spores hyaline, cylindric or subfusoid or suballantoid, smooth, nonamyloid, with very thin walls, in print white or nearly so; basidia normal, often with locally thickened wall at their apices, and then often transformed into pseudoparaphyses or even inconspicuous cystidioles, but true cystidia and pseudocystidia wanting ; stipe lateral, compressed ; context soft, almost leathery ; hyphae partly with thin, partly with thick wall, nonamyloid, with clamp connections, hyaline. On wood.

Development of the carpophores Unknown.

Area : North America.

Limits : The structure of the pileus apparently separates it strictly from all related genera.

State of knowledge : The only species referable to this genus is rather well known, yet, there are certain items that need further observation (development of the carpophores, characters of the fresh specimens including spore print in thick layer observed before dehydration).

SPECIES

A. dealbatus (Berk.) Sing. (Panus, Berk.; Panellus, Murr.).

GENERA OF UNCERTAIN AFFINITY

Asterochaete (Pat.) Bond. & Sing., *Ann. Mycol.* 39:58. 1941. This genus is very similar to *Polyporus* sensu stricto but differs in having setulae that are more or less colored and branched, sometimes almost dichophysoid, or somewhat in the manner of the setulae of *Erioclades brasiliensis*. If *Polyporus* will eventually become a genus of the *Agaricales*, then, consequently, *Asterochaete* will also enter that group. On the other hand, the setulae are more like similar formations in the *Aphyllophorales* than anything in the *Agaricales*. A more profound study of the species concerned should provide the additional data needed to answer the question about the position of *Asterochaete*. These species are: *A. cinnamomeosquamulosa* (Henn.) Bond. & Sing. (Polyporus, Henn.); *A. coracina* (Murr.) Bond. & Sing. (Polyporus, Murr.); *A. megalopora* (Mont.) Bond. & Sing. (Polyporus, Mont.); *A. princeps* (Berk. & Curt.) Sing. (Favolus, Berk. & Curt.); *A. rusticeps* (Berk. & Br.) Bond. & Sing. (Polyporus, B. & Br.). The type species is *A. megalopora*.

Porodisculus Murr. *North Am. Fl.* 9: 47. 1907, (*Enslinia* Fr. 1849 non Reichenb. 1827; *Porodiscus* Murr. 1904 non Grev. 1863). « Carpophore small, annual, tough, epixylous, erumpent from the lenticles of dead branches; stipe attached to the vertex of the pileus, usually curved at maturity; context white, fibrous, tubes cylindrical, short, one-layered, mouths constricted; spores... smooth, hyaline ». Murrill 1907. The type species is *P. pendulus* (Schw.) Murr. (Peziza, Schw.; Sphaeria pocula Schw.; Polyporus cupulaeformis Berk. & Curt.). It has been restudied by Singer (1945). The spores are nonamyloid and by no means round (Murrill's erroneous indication is copied from Overholts who, in turn cited Cooke, a most unreliable source); the covering of the pileus is dichophysoid, somewhat as in *Dictyopanus pusillus* and *Asterotus dealbatus*; the « stipe » indicated by Murrill is, of course, a pseudostipe. The dichophysoid covering suggests some affinity with *Asterotus* since the spores are cylindric-allantoid, not short as in the other genera with the same surface structure. The poroid representatives of the *Lentineae* have not yet

been finally inserted in the classification adopted in the present work. *Porodisculus* would probably enter the same unit (family, or tribus) as the genus *Polyporus*, and perhaps *Asterochaete, Pseudofavolus*, and *Mycobonia*.

Tribus **HEMIMYCENEAE** Sing.

Sydowia **2** : 30. 1948.

Type genus : *Hemimycena* (Sing.) Sing. (= *Marasmiellus* Murr.).

Characters : Basidia normal, i. e. devoid of carminophilous granulosity ; habit of the carpophores collybioid, omphalioid, mycenoid, or marasmioid, in the latter case often more or less pleurotoid, i. e. with eccentric or reduced stipe, in certain forms even the hymenophore is reduced and the whole carpophore becomes stipitate-vesiculose or cup-shaped (pezizoid) : epicutis of the pileus (equivalent with outer surface of the cups) not containing any amyloid or pseudoamyloid elements ; trama nonamyloid ; spores nonamyloid ; epicutis of the pileus and stipe often well differentiated (hairs, diverticulate hyphae, hymeniform structures, dermatocystidia, etc.) : gloeocystidia sometimes present ; cuticular layer of the pileus sometimes consisting of hyphae imbedded in a gelatinous layer ; black rhizomorphs sometimes present ; hyphae usually with clamp connections at least in normal forms; latex present or absent (more often absent). On a great variety of substrata, on dead and living vegetable matter, very frequently on wood, foliage, dead herbaceous stems, on sand and humus, roots, etc., also in deep moss, not parasitic on other fungi.

KEY TO THE AGARICOID GENERA

pileus and stipe differentiated ; hymenophore ± developed

A Walls of the spores and the basidia thickened and not always simple in the spores which are somewhat cream colored, not quite hyaline under the microscope because of a yellowish endosporium ; hymenopodium gelatinized.
50. *Phaeomycena*

A. Not combining these characters

B Spore print pure white or slightly creamy, not pinkish.

C Pileus viscid, with hymeniform epicutis or epithelium, often covered by the patches of an inner veil with heteromerous structure, or without an inner and an outer veil ; hairs on pileus and stipe none. Habit collybioid, sometimes very large and thick 43 *Oudemansiella*

D. Epicutis of the pileus consisting of a hymeniform layer, or an epithelium, or of distinctly diverticulate hyphae, or of dermatocystidia alone, but in the latter case the pileus not gelatinized (viscid) at all.

E. Pileus and stipe macroscopically hairy, pilose or floccose-scaly (furfuraceous), microscopically the hairs dispersed among a hymeniform epicuticular layer; basidia and cystidia very large; spores smooth, very broad, subglobose or piriform-ellipsoid; habit of the carpophores that of a rather large *Collybia* or *Marasmius*. 44. *Xerula*

E. Pileus and stipe not macroscopically hairy or floccoso-scaly, or else the pileus is devoid of a hymeniform layer and the spores, basidia, and cystidia are not as described above; habit variable within the limits of the tribus, but rarely does the carpophore reach large dimensions.

F. Spores globose and smooth with very large hilar appendage, or globose and spiny-echinate.

15. *Mycenella*

F. Spores not as described above.

G. Pileus without a palisade of dermatocystidia and without an epithelium, the epicutis merely consisting of diverticulate repent, irregular but filamentous, or at least elongated hyphae, or irregular branched bodies, rarely of hair-like bodies or dermatocystidia; septa usually clamped in normal 4-spored forms; habit collybioid, mycenoid, marasmioid, omphalioid (rarely almost clitocyboid), or pleurotoid (if the pileus is glutinous or stipe with pedestal see *Mycena*, p. 350). 46. *Marasmiellus*

G. Pileus with a palisade (or hymenium) of dermatocystidia or with an epidermium; clamp connections present or absent (absent especially in temperate species).

H. Pileus with long dermatopseudocystidia, projecting from gloeovessels or laticifers.

51. *Lactocollybia*

H. Pileus without dermatopseudocystidia and gloeovessels; instead, the epicutis of the pileus is made up of a hymeniform layer, sometimes interspersed with hairs, or else an epithelium forms the epicutis (see *Marasmieae*, genera *Pseudobaeospora* and *Marasmius*.

D. Pileus without a hymeniform epicutis and also without diverticulate hyphae, dermatocystidia none unless the cuticle of the pileus is gelatinized.

I. Pileus viscid, soft-fleshy; stipe more or less velvety, habit collybioid; dermatocystidia present on the pileus.

I. Pileus not viscid, and not combining the other characters indicated above.

J. Cystidia conspicuous on the sides of the lamellae, with a very broad base and acute apex; lamellae not strongly decurrent. (see *Marasmius*, p. 321)

J. Cystidia on the sides of the lamellae conspicuous, inconspicuous, or absent, never shaped as described above; lamellae non-decurrent or decurrent.

K. Pigment intracellular (or membranal); black rhizomorphs none, cuticle and trama non-gelatinized (see *Marasmiellus*).

K. Pigment intercellular or incrusting the walls of the hyphae, brown; black rhizomorphs present or absent and if they are absent, the hyphae of the pellicle of the pileus imbedded in a gelatinous mass. 47. *Micromphale*

B. Spore print distinctly pink. 49. *Macrocystidia*

KEY TO THE GENERA OF THE REDUCED SERIES

(hymenophore absent; carpophore reduced)

A. Pileus not inflated; stipe present or absent.

B. Pileus not cup-shaped (pezizoid), centrally, eccentrically, laterally, or dorsally stipitate. 50. *Cymatella*

B. Pileus cup-shaped (pezizoid), the hymenium on the concave side of the cup, the sterile outside pilose; stipe none. 53. *Flagelloscypha*

A. Pileus inflated, stuffed to hollow, the sterile and the fertile portion of the pileus not morphologically predetermined; stipe present. 54. *Physalacria*

43. OUDEMANSIELLA Speg.

An. Soc. Cient. Arg. **12**: 24. 1881.

Type species: O. platensis (Speg.) Speg.

Syn.: Oudemansia Speg., *An. Soc. Cient. Arg.* **10**: 280. 1880.
Mucidula Pat., *Hymen. Eur.* p. 95. 1887.
Phaeolimacium Henn. in Warburg, *Monsunia* **1**: 14. 1900.
Chamaemyces (Batt.) ex Earle (non Batt.), *Bull. N. Y. Bot. Gard.* **5**: 446. 1909 [**].
? *Coprinopsis* Beeli, *Bull. Soc. R. Bot. Belg.* **61**: 98. 1928 (non Karst. (1881).

[**] Earle indicates as the type of this genus *Armillaria fracida* (Fries) (*Syll.* **5**: 86). This, in our interpretation, is a proposed lectotype rather than the legitimate type species of a new genus. In fact, Earle's genus is not a perfectly new genus but can be interpreted as a modernization of Battarra's genus, or — in accordance

Characters : Habit of the carpophores collybioid; carpophores rather large, often pigmentless or almost so, or with a brown to olive pigment; pileus often rather large, viscid to glutinous; cuticle of the pileus bearing a hymenium of broad epicuticular elements above a gelatinized layer; the epicutis often partly covered by a velar layer, the whole cuticle (pellicle) easily separable from the context of the pileus; lamellae thick, in youth often obtuse at the edge, neither free nor decurrent, broad; spore print pure white; spores, basidia and cystidia gigantic, spores globose or subglobose, smooth, or echinate (as in *Laccaria* and *Mycenella)*, nonamyloid, with often thickened but always continuous wall: basidia normal; cystidia broad; hymenophoral trama regular; stipe usually mostly white, often radicate (with a pseudorrhiza), with or without a veil, if veiled, the veil often double: context soft-fleshy, white, unchanging, consisting of hyphae which are nonamyloid, with clamp connections, more rarely without them.

Development of the carpophores : O. mucida and *O. Canarii* are hemiangiocarpous (see Fischer 1909 and Corner 1934).

Area : Tropics and temperate zones, not transgressing the northern limit of the area of *Fagus.*

Limits : This genus can be separated from all related genera by the characters indicated in the keys and the generic description.

State of knowledge : All four species are completely known.

with the valid rules of nomenclature — a new status of a section established by Fries. Earle himself said : « This is *Armillaria* § *Collybiae-annulatae* of the *Sylloge* » If so, the lectotype of this section would automatically become the lectotype of *Chamaemyces*. Earle's proposal is not good. In the first place, it is in contradiction with his intention because *A. fracida* is based on one of Secretan's descriptions, *Agaricus macidus* (typographical error for *A. mucidus*) which was a misdetermination of that species describing *Drosella* rather than *Oudemansiella*, further on Battarra's picture (which is an *Agrocybe* or *Psathyrella*) and on a plate in *Flora Danica* (which is a *Mycena* which has been drawn in one figure with an annulus — a mistake?) Both these pre-Friesian pictures are inconclusive as far as their determination is concerned, and the description of *A. fracida* refers to *Drosella* which is not what Earle expected. In fact *Drosella* has yellow spores whi1e Fries' *Armillaria* is described as having white spores, and the only white spored well-known species of the section indicated and described by Earle, Saccardo and Fries, is *Oudemansiella mucida*. If so, this latter species should be recognized as the lectotype of the section « *Collybiae annulatae* » and consequently of the genus *Chamaemyces*. This makes *Chamaemyces* a synonym of *Oudemansiella* which is in line with the whole text in Earle who describes the spores as white and indicates *Mucidula* Pat. as a synonym of *Chamaemyces*.

Practical importance : Some species may occasionally be mildly parasitic on trees weakened by other factors; all but one have been tested for edibility, and have been found to be good, palatable food.

SPECIES

O. mucida (Schrader ex Fr.) Hoehnel (Agaricus, Fr.; Armillaria, Quél.; Collybia, Quél.; Lepiota, Schröter; Mucidula Pat.); *O. Canarii* (Jungh.) Hoehnel [Agaricus, Jungh.; Collybia alphitophylla (Berk. & Curt.) S. Ito & Imai; Amanitopsis cubensis (Berk. & Curt.) Sacc.; Oudemansia platensis (Speg.) Speg.; Oudemansiella, Speg.; Armillaria cheimonophila (Berk. & Curt.) Sacc.; Phaeolimacium bulbosum Henn.; Pluteus macrosporus Henn.]; *O. radicata* (Relh. ex Fr.) Sing. (Agaricus, Fr.; Collybia, Quél.; Mucidula, Boursier; Clitocybe megalospora Clements); *O. echinosperma* Sing.

KEY TO THE SPECIES

A. Veil present; pigment absent or scarce, rarely (in *O. Canarii*) abundant
  B. Constantly annulate, without remainders of the veil on the pileus; area of the beech, mostly on *Fagus silvatica*, *F. orientalis*, and *F. grandifolia* but occasionally also on other frondose trees. *O. mucida*
  B. Rarely truly annulate but — unless the weather is too wet — usually with fragments of the veil on the pileus as in *Amanita*. On tropical and subtropical trees south of the area of *Fagus* in America, Asia and Oceania. *O. Canarii*

A. Veil none; pigment usually abundant, even on the margin of the pileus
  C. Spores smooth. Occurring in a wide area, in the temperate and tropical zone. *O. radicata*
  C. Spores echinate. Southern Brazil, Paraguay, Argentina. *O. echinosperma*

44. XERULA R. Maire

Publ. Junta Cienc. Nat. Barcelona, p. 66. 1933

Type species : *Xerula longipes* (Bull. ex Fr.) R. Maire.

Characters : Habit of the carpophores collybioid; pileus and stipe pilose or floccose, non-viscid, pigmented; lamellae adnexed; cuticle hymeniform and with long hairs, many of them macroscopically visible; spore print pure white; spores hyaline, smooth, medium sized

sides of the lamellae; hymenophoral trama subregular, consisting of nonamyloid, somewhat interwoven hyphae with clamp connections; context mostly white, fleshy to slightly tough. On humus, buried wood, and on logs.

Development of the carpophores: Not studied recently.

Area: Approximately same as in *Oudemansiella*.

Limits: The limits of this genus are obvious as far as all genera except *Oudemansiella* and *Mycenella* are concerned. *Xerula* is exactly intermediate between these two genera. Boursier has thought it possible to include *Xerula* in what he called *Mucidula*, i. e. *Oudemansiella*. Heim, Konrad & Maublanc, Kuhner, Maire, Romagnesi and Singer have disagreed. These authors believe that *Oudemansiella* and *Xerula* are distinct. As for the delimitation of *Mycenella* see that genus.

State of knowledge: The species of *Xerula* are rather well known. Yet, there are some differences of opinion regarding the number of species. While admitting four species at present, the author does not want to take sides as far as the final taxonomic status of *X. Caussei* and *Pleurotus aureotomentosus* is concerned.

Practical importance: Hardly any.

SPECIES

Xerula pudens (Pers. ex S. F. Gray) Sing. (Agaricus radicatus pudens Pers. 1799; Agaricus pudens Pers. 1825; Gymnopus pudens S. F. Gray 1821; Agaricus longipes Bull. ex Fr. 1836; Collybia, Quél.; Marasmius, Quél. 1888; Mucidula, Boursier; Xerula, R. Maire; Mycenella, Romagnesi); *X. Caussei* R. Maire (Mycenella, Romagnesi); *X. chrysopepla* (Berk. & Curt.) Sing. [Lentinus, B. & C.; Gymnopus, Murr.; Omphalia scabriuscula (Peck) Sacc.; Tricholoma lacunosum (Peck) Sacc.; Collybia, Peck 1891; Marasmius aculeatus Pat., Lepiota aurantiosquamosa, Charles]. Also *X. lachnocephala* (Pat.) Sing. (Collybia, Pat.) — but *Pleurotus aureotomentosus*, Kalchbr. may be an older name for it unless it is a synonym of *X. chrysopepla*).

KEY TO SPECIES

A. Pileus hairy, not bright yellow to orange ... *X. pudens* and *X. Caussei*

A. Pileus floccose, ochraceous to orange ... *X. lachnocephala*, *X. chrysopepla*

45. MYCENELLA (Lange) Sing.

Notulae Systematicae Sect. Crypt. Inst. Bot. Acad. Sc. U. S. S. R. fasc. **10-12**: 9. 1938.

Type species: *Mycena (Mycenella) margaritospora* Lange.

Syn.: *Mycena* subg. *Mycenella* Lange, *Dansk Bot. Ark.* **1** (5): 46. 1914.
Mycena subg. *Paramycena Hemimycena* sect. *Mycenella* Kühner, *Genre Mycena*, p. 609. 1938.
Marasmius sect. *Laccariosporae* Sing. *Beih. Bot. Centralbl.* Abt. B **56**: 163. 1936.

Characters: Habit of the carpophores mycenoid to almost marasmioid but rather small (diameter usually not more than 20 mm), not pilose-hirsute but often pruinose or pubescent, dry or slightly sticky, not glutinous, pigment usually present but not bright colored, usually gray or pale to dark fuscous or melleous; lamellae subfree to adnate, white to gray, horizontal or initially somewhat ascendant; epicutis consisting of diverticulate hyphae, or hymeniform, rarely with interspersed hairs; hymenophoral trama regular to subirregular or subinterxmixed; spore print white to light cream color; spores small to large, usually spiny, rarely smooth, always with a very large hilar appendage; basidia without carminophilous granulation, normal in size for this tribus, 2-spored or 4-spored, rarely 1-spored or 3-spored; cystidia present on the sides of the lamellae; spores and hyphae nonamyloid; clamp connections present or absent; plants often homothallic-diploid or parthenogenetic. On various dead and living parts of *Cormophyta*, or on humus.

Development of the carpophores: Unknown.

Area: Northern temperate zone according to the present data but the existence of *M. Cyatheae* shows that these species can at least adapt themselves to hosts from outside this area, and a wider distribution can be anticipated.

Limits: Romagnesi has very ably pointed out that *Mycenella* and *Xerula* are closely related (*Bull. Soc. Myc. Fr.* **56**: 59-65. 1940), in fact he thinks that these genera are not divided by a hiatus («il n'y a aucune solution de continuité entre ces deux genres»), and that they should be combined under the name *Mycenella*. The hairy species with *Collybia* habit with constantly smooth spores do not seem to be so inseparably linked with the small mycenoid species with echi-

rulas is nothing but an extreme of the (microscopical) hairs observed in *Mycenella*, and it may be said that if smooth spores are admitted in *Mycenella (M. salicina)* they should also be admitted in the large spored forms *(Xerula)*. But since these characters coincide with the general habit of the carpophores, and therefore a correlation between two important characters exists whereby one of them is basic in the Friesian sense, the author thinks that at present the taxonomist cannot go beyond an acknowledgment of Romagnesi's demonstration of affinity between the two genera. They can be kept as separate genera but if ever the combination of these genera into one should become desirable on the basis of more definitely intermediate species, the resulting genus must be called *Xerula* and not *Mycenella* since the author has published the latter as a genus in 1938 while *Xerula* was published validly in 1933.

State of knowledge : Five species of *Mycenella* are now known, not counting the species that might be distinguished on the basis of differences in sexuality. These species can be considered as well known.

Practical importance : Some species may be mildly parasitic.

SPECIES

M. salicina (Vel.) Sing. (Mycena, Vel.) ; *M. lasiosperma* (Bres.) Sing. (Mycena, Bres. ; ? Mycena margaritispora, Lange) ; *M. bryophila* (Vogl.) Sing. (Mycena, Vogl.) ; *M. Cyatheae* (Sing). Sing. (Marasmius, Sing. 1936) ; *M. Kuehneri* Romagnesi ; obviously also *Mycena trachyspora* Rea sensu A. H. Smith and probably *M. nodulosa*, A. H. Smith.

KEY TO THE SPECIES

A. Spores smooth. *M. salicina*

A. Spores echinate.

  B. Cystidia at the apex finely ramulose or cristate *M. lasiosperma*

  B. Cystidia not lacerate at the apex.

    C. Spores 14-16 µ in diameter ; basidia 55-60 × 14-15 µ ; cystidia enormous : 100-120 × 13-20 µ (according to Romagnesi). *M. Kuehneri*

    C. Spores smaller ; basidia smaller , cystidia smaller.

      D. Margin of the pileus and lamellae cinereous , lamellae adnexed and long-striate-decurrent at the apex of the stipe which is 2-4 mm thick and somewhat tough. On living *Cyathea*. *M. Cyatheae*

      D. Not so. *M. bryophila*

46. MARASMIELLUS Murr.

North American Flora **9** (4) . 243. 1915, em. Sing. (1948).

Type species : M. juniperinus Murr.

Syn. : Mycena subg. *Hemimycena* Sing. *Ann. Mycol.* **34** : 350. 1936 ; *Beih. Bot. Centralb.* Abt. B **56** : 160. 1936.
Mycena subg. *Paramycena* Kühn *C. R. Acad. Sciences* **203** : 1287. 1936.
Hemimycena (Sing) Sing., *Rev Myc* **3** : 194. 1938.

Characters : Habit mycenoid, omphalioid, or collybioid to marasmioid, rather rarely pleurotoid and then small with eccentric curved stipe; pigment present or absent, bright or dull, intracellular or incrusting (or both); pileus usually rather thin (membranaceous) and more or less transparently striate, usually hygrophanous, non-viscid or very slightly lubricous; epicutis of the pileus diverticulate, or with hairs or dermatocystidia; lamellae ascendant or horizontal or descendant, subfree, sinuate, adnexed, adnate, or decurrent; often reduced to mere veins or rugosities; in the species with distinct lamellae, the hymenophoral trama is regular to irregular, or sometimes rather intermixed (but not differentiated into an inner regular mediostratum and an outer irregular layer); spores hyaline, smooth, rarely angular to stellate, nonamyloid; basidia normal, i. e. without carminophilous granulosity; cheilocystidia present or more rarely absent; cystidia on the sides of the lamellae present or absent; gloeocystidia never present as the only cystidioid bodies in the carpophore; stipe thin, fragile or tough (cartilaginous to chordaceous), usually with a soft stuffing or narrowly hollow, insititious or not, without latex, often separated from the pileus by a separating zone consisting of smaller elements (the stipe consequently « distinct » from the pileus); context of the pileus fleshy-membranaceous to membranaceous-tough, reviving or non-reviving, the hyphae of the pileus never amyloid, those of the stipe rarely slightly amyloid (much less so than in *Mycena* — except the species where the reaction is obscured by rich pigmentation, e. gr. *M. androsaceus* —, *Poromycena* and *Pseudobaeospora*), with or without a metachromatic discoloration of the tissue of the stipe to lilac pinkish with cresyl blue; the tissue often pervaded by conducting elements (oleiferous hyphae ?); clamp connections present or very rarely absent (in normal diploid heterothallic forms probably always present). On wood, herbaceous stems, fruits, leaves, needles, in deep moss, and on other dead or live vege-

Development of the carpophores : Kühner states generally for *Mycena* (which in his sense includes *Marasmiellus* except for the section *Rameales*) that « while waiting for new researches, it seems to be wise to consider the Mycenas as gymnocarpous, or, at the most, pseudo-angiocarpous in certain cases ». Kavina said, the Mycenas are hemiangiocarpous, or at least gives data to that effect, but Kühner doubts these indications as based on material not young enough. There is nothing known on the development of the *Rameales*.

Area : Cosmopolitan.

Limits : The limits of this genus are interesting in several regards, and in need of comment beyond the text of the keys and the generic description.

(1) *Mycena :* This genus has, as a rule, amyloid spores and amyloid context. There are only very few exceptions, and these do not refer to groups close to *Marmasmiellus* but rather belong to very characteristic sections of the genus *Mycena* from which they are inseparable. These groups are mainly the glutinous species and the species with basal disc. Considering this, correlation of the two characters (amyloid context and amyloid spores) is quite usable for the separation of *Mycena* and *Marasmiellus*, and consequently the hiatus between these genera are abrupt enough to warrant generic separation. In some species of some sections in *Marasmiellus*, the tissue of the stipe is very weakly amyloid, but, in combination with the other characters, especially the nonamyloid spores, these species can immediately be recognized as *Marasmiellus*.

The only species that seem to contradict the rules indicated above, are *Mycena scabripes* (Murr.) Murr. and *M. trichoderma* Kühner, which are intermediate between *Mycena* and *Marasmiellus* insofar as the spores are amyloid but the hyphae nonamyloid. The author has only a very scanty personal knowledge of these species which were put into a group of his heterogeneous section *Spuriae* by Kühner. They do not fit into any of the genera of the *Myceneae* and may well be considered as a new genus related to *Hydropus*. More detailed studies on this subject are desirable.

(2) *Poromycena :* The difference of the iodine reaction is very important ; the epicutis of *Poromycena* does not show any diverticulate hyphae, dermatocystidia, etc. whereas in *Marasmiellus*, the epicutis is always diverticulate if the tissue is even very weakly amyloid in certain portions.

(3) *Marasmius :* The section *Rameales* of *Marasmiellus* was origi-

nally a section of *Marasmius* from which it was transferred to *Marasmiellus* because of the close affinity between it and certain other sections of *Marasmiellus*. Among the true *Marasmii*, there are only three sections that are comparable with the *Rameales*, viz. *Epiphylli*, *Androsacei* and *Alliati*. The latter can be discarded immediately because of their characteristic epicutis which does not occur in *Marasmiellus*. The section *Androsacei*, however, has an epicutis similar to that of the *Rameales* of *Marasmiellus*, yet the appearance and structure of the stipe in the *Androsacei* is more like that of the other *Marasmii* than of *Marasmiellus*. The reaction of the tissue of the stipe with iodine is definitely positive in at least one species, and in the species where it is possibly negative, it cannot be demonstrated because of the abundance of the pigment which obscures any possible change in color. It appears to the author that the *Rameales* and the *Androsacei* are probably related but there is a much more abrupt hiatus between them than between the *Rameales* and the other *Marasmielli*, and between the *Androsacei* and the other *Marasmii*. The non amyloid species of the *Epiphylli* differ from the *Marasmielli-Rameales* with occasional spherocysts in the epicutis by their distinct cystidia.

(4) *Omphalina*: Some of the species of *Marasmiellus* are extremely similar, in external appearance, to the species of *Omphalina*. This is especially true for *M. icterinus* and *M. subchrysophyllus* but also for some of the white species which were formerly considered as *Omphaliae*. The genus *Omphalina* as it is understood at present, differs from all the *Marasmielli* in having no cystidia (and cheilocystidia) and smooth repent hyphae in the epicutis of the pileus (no hairs, and no dermatocystidia); many of the species of *Omphalina* have clampless septa, and the pigment is always incrusting. The hymenophoral trama is rather characteristic in some white and bright colored species that, because of their color and appearance may be taken for *Marasmiellus*. Such species are: *O. Postii*, *O. brevibasidiata*, *O. Josserandii*.

(5) *Clitocybe*: It seems strange to compare the genus *Clitocybe* with *Marasmiellus*, yet there are species in both genera which, because of their external appearance, might rather be expected to have the microscopical characters of the other genus — which, however, they do not. *Omphalia ignobilis* Joss. has been transferred to *Mycena* by Kühner but it has none of the anatomical or chemical characters of that genus, and in spite of its external similarity with the *Marasmielli* of the section *Candidi*, it is, in the author's opinion, nothing but

an extremely small and thin *Clitocybe*. In reverse, *Marasmius substenophyllus* Murr. had to be transferred to *Marasmiellus* because of the microscopical characters which clearly refer it to the section *Candidi* as an exceptionally large and thick species that, on the basis of certain collections, might easily pass as *Clitocybe* if the anatomical characters are neglected. In spite of these two cases, the genera *Marasmiellus* and *Clitocybe* can easily be distinguished and do not present any actual problems of taxonomic order.

(6) *Collybia :* Kühner considered as belonging in the section *Rameales* of *Marasmius* (here *Marasmiellus*) a species, *Marasmius candidus*, which is distinguished from all other species of that group in having smooth epicuticular hyphae. About the position of this species, see under *Collybia*. A similar case is *Collybia pseudoclusilis* Konr. & Favre. This species may also be a *Marasmiellus* rather than a *Collybia*. Since, consequently, all cystidiate species of *Collybia* have either finally or tentatively been excluded from *Collybia*, we can now say that *Collybia* never has cystidia on the sides of the lamellae.

(7) *Mycenella :* Kühner considered this genus as section of *Paramycena-Hemimycena* which is the same as *Marasmiellus*. It is true that both genera have many characters in common. The epicuticular structure is analogous and the presence of cystidia in *Mycenella* is not in contradiction with the diagnosis of *Marasmiellus*. Nevertheless, the spores are of a very different type, and there are also several less important anatomical characters that make it desirable to separate the two genera. In addition to this, there is also the fact that *Mycenella* is closer to *Xerula* than to *Marasmiellus :* consequently, a combination of *Marasmiellus* and *Mycenella* would logically include *Xerula*. In these limits, the genus *Marasmiellus* does not appear to be a homogeneous unit, and in the author's opinion, would merely represent a compound genus of the Friesian pattern, only this time based on chemical instead of macroscopical characters. If taxonomists should now favor to neglect such hiatus as exist between the genera *Xerula*, *Mycenella*, and *Marasmillus*, we shall find it impossible to maintain any genera in the *Agaricales*, and soon slide back to genera like *Marasmius* but in a much wider sense, comprising most of the genera of three tribus. It is felt that this would be to no avail for taxonomy, and more than one step backwards.

(8) *Nothopanus : Marasmiellus tropicalis* is rather close to the genus *Nothopanus*.

(9) *Micromphale :* This genus, though close to *Marasmiellus* and

Collybia, differs clearly in the characters indicated in the keys, see also p. 303.

The above comments on the delimitation of the genus *Marasmiellus* are seemingly in contrast with Kühner's and A. H. Smith's taxonomic proposals. While this may be so, the solution suggested in the present book is by no means in opposition to the opinions published by these distinguished authors. On the contrary, the reader should appreciate that Kühner as well as Smith had as their subject a monograph of the genus *Mycena* such as it was traditionally understood, and their results — though naturally not aiming at a new generic subdivision of the entire complex of genera affected, — are largely in agreement with the author's conception. In some cases, Kühner was the first to show certain affinities, and in other cases Kühner's and the author's parallel proposals appeared the same year. The main difference between the author's conception and that of the authors named above, is the fact that some of the sections and subgenera used by them, are considered as genera in the present work. The subject of this conspectus is a presentation of modern taxonomy in the *Agaricales*, and this particular aim is not furthered by useless concessions to the conservatives as much as this may appear to be desirable in floras, monographic studies and papers of purely popular appeal.

Note: The transfer of the *Rameales* to *Marasmiellus* has unfortunately had the most shattering effect on the nomenclature of that genus. These effects were not foreseen when the incorporation of the section *Rameales* was first proposed by the author. Immediately afterwards, in preparation for the present analysis of the genera of the *Agaricales*, the author studied the type specimen of the type species of *Marasmiellus*, and there cannot be the shadow of a doubt that it belongs in the section *Rameales*. This makes it necessary to prefer the generic name *Marasmiellus* to *Hemimycena*, a genus in which most of the necessary combinations already had been made. However, since the majority of the phytopathologists and even many mycologists have not yet used the combinations with *Hemimycena* (partly because the publication containing the new combinations, appeared, against the author's wishes, during the war where it was not available to most agaricologists) no general consent has been achieved. It is better to transfer all the species to *Marasmiellus* now than to think of conservation of the name *Hemimycena*, or to let things go without any recommendations.

State of knowledge : The species of *Marasmiellus* have been studied by R. Kühner and A. H. Smith during the last decennium. The main subdivisions as indicated below, are still those proposed by Kühner (with some slight emendations where this seemed advisable for nomenclatorial reasons, and with certain additions published after Kühner's papers were published). These small and often overlooked fungi will require more and more special studies, especially in the tropics and in generally neglected regions such as Australia and Eastern Asia. It is not impossible that as a result of such additional studies, the species of *Marasmiellus* will be rearranged in a revised classification, but under the present circumstances, and with the present data at hand, the genus *Marasmiellus* appears as a very convenient taxonomic link between various other genera with the sections and subsections adopted here showing the gradual approach to some of them, especially *Marasmius*, and *Mycena*.

Within *Marasmiellus*, the author admits 58 species, which include all the species inserted here or in corresponding groups by Kühner, A. H. Smith, or the author himself.

Future research will also take into consideration such problems as cytology, sexuality, and specialization. While Kühner has begun to study the sexuality and the cytological characters of many *Marasmielli*, little is known at present about the specialization of these fungi. The specialization seems to follows family lines rather than generic lines or species as far as the hosts are concerned, e. gr. *M. candidus* occurs on *Scrophulariaceae ; M. pseudocrispulus* on *Compositae*. Both these families are apparently among the more recent ramifications of the plant world, and it is therefore likely that the specialization of the species of *Marasmiellus* is also of rather recent origin. This is not surprising inasmuch as the specialization of the fungi regarding their hosts is by no means a generic character. In fact, we find, side by side with strongly specialized species, others that are truly omnivorous, such as *M. semiustus*.

Practical importance : Marasmielli are responsible for at least one form of the sugar cane root disease which is not a very specific disease but, as far as the pathogenic organism is concerned, must be considered as a compound of various diseases with similar symptoms. A serious disease of palms, especially the coconut palms, is caused by *Marasmiellus pigmentatus* (Bliss) Sing. Other species can be observed attacking and killing grass and sedges, and it is conceivable that some of these species also damage the cereals. The species

of the section *Hiemales* often grow on living trees, on the bark, but they do not seem, as a rule, to damage the trees seriously.

SPECIES

Sect. 1. **CANDIDI** (Kühner 1926 ut sect. generis *Mycenae*) Sing.; (*Lacteae* Konr. & Maubl., Kühn. 1938). Carpophores perfectly pigmentless; cystidia, even cheilocystidia often absent; stipe often « grafted » (implanted) in the substratum, or subradicant and lacerate into rhizoid fibrils, usually pruinate, continuous with the pileus, with absolutely nonamyloid tissue, and with non-metachromatic hyphae when stained with cresyl blue; lamellae subfree to more often decurrent; trama of the lamellae distinctly irregular or intermixed. Not, or only occasionally, on the bark of living trees.

Type species : M. candidus (Bres.) Sing.

Subsection Typici Kühn. (1938). Lamellae initially ascendant or horizontal with concave arcuate edge; hyphae of the pileus made up of thin (smaller than 13 µ) hyphae; cystidia always distinct.

Type species : Hemimycena lactea (Pers. ex Fr. sensu Lange) Sing. [= M. delicatellus (Peck) Sing.].

M. gypseus (Fr. sensu Ricken) Sing. (Mycena, Gillet); *M. Rickenii* (A. H. Smith) Sing. (Mycena, A. H. Smith; Mycena lactea sensu Rick.); *M. delicatellus* (Peck) Sing. [Collybia, Sacc.; Hemimycena lactea (Pers. ex Fr. sensu Lange) Sing.; Mycena, Quél.; Mycena ludia (Fr.) sensu Ricken; Mycena lactea var. pythia (A. & S. ex Fr.) Quél. sensu Pat.; Mycena crystallina Peck]; *M. pseudolacteus* (Kühn.) Sing. (Mycena, Kühn.); *M. cephalotrichus* (Josserand) Sing. (Omphalia, Josserand; Mycena, Kühn.); *M. albidus* (Murr.) Sing. (Gymnopus, Murr.).

Subsection Hirsuti Kühn. (1938). Lamellae not as indicated above; pileus with long hairs (at least 30-60 µ long and sometimes assuming the character of dermatocystidia); stipe also pilose.

Type species : M. mauretanicus (R. Maire) Sing.

M. angustisporus (Josserand) Sing. (Omphalia, Josserand; Mycena, Kühner); *M. epibryus* (Sing.) Sing. (Hemimycena, Sing. 1943); *M. mauretanicus* (R. Maire) Sing. (Omphalia, R. Maire; Mycena, Kühn.); *M. crispulus* (Quél. sensu Kühner) Sing. (Omphalia, Quél.; Omphalina, Quél.; Delicatula, Pat.; Mycena, Kühn.); *M. pseudocrispulus* (Kühn.) Sing. (Mycena, Kühn.; Hemimycena, Sing. 1943).

Subsection Nudi Kühn. (1938). Lamellae as in the subsection

Hirsuti, i. e. usually distinctly arcuate-decurrent and rather descendant than ascendant; cystidia and even cheilocystidia often lacking; hairs on the pileus and on the stipe absent, and replaced by diverticulate hyphae.

Type species : As in section.

M. gracilis (Quél. sensu Sacc.) Sing. (Mycena Kühn.; Omphalia, Quél., Sacc.); *M. pseudogracilis* (Kühn. & Mre.) Sing. (Mycena, Kühn. & Mre.; Hemimycena, Sing. 1943); *M. crispatus* (Kühn.) Sing (Mycena, Kühn.); *M. candidus* (Bres.) Sing. (Omphalia, Bres.; Mycena, Kühn.; Hemimycena, Sing. 1943); *M. delectabilis* (Peck sensu A. H. Smith) Sing. (Mycena, Sacc., A. H. Smith, Kühn.); *M. Mairei* (Gilbert) Sing. (Omphalia, Gilbert; Mycena, Kühn.); *M. substenophyllus* (Murr.) Sing. (Marasmius, Murr.). Perhaps in this section *M. buccinulus* (Speg.) Sing. (Clitocybe, Speg.).

Sect. 2. **DEPAUPERATI** Sing. (1943 ut sectio *Hemimycenae*). Habit mycenoid; lamellae ascendant, pigment of the pileus gray; spores ellipsoid; cheilocystidia and cystidia on the sides of the lamellae absolutely none; hymenophoral trama subirregular; hyphae of the epicutis of the pileus diverticulate.

M. depauperatus (Sing.) Sing. (Hemimycena, Sing.).

Sect. 3. **XANTHOPHYLLI** Sing. Habit omphalioid; pileus and stipe confluent; lamellae descendant, distinctly decurrent, or with decurrent ridges, distinctly yellow or brownish; spores ellipsoid; cheilocystidia present, not lacerate (broom like) at the apex; other cystidia none; hymenophoral trama subirregular; hyphae of the cuticle at least partly interwoven, not (or not distinctly) diverticulate.

Type species : M. subchrysophyllus (Murr.) Sing.

M. icterinus Sing.; *subchrysophyllus* (Murr.) Sing. (Omphalina, Murr.). *M. Stuckertii* (Speg.) Sing. (Omphalia, Speg.); *M. pulchellus* (Speg.) Sing. (Clitocybe, Speg.).

Sect. 4. **RAMEALES** Lange (1921, ut sect. *Rameali* gen. *Marasmii*). Habit omphalioid to collybioid marasmioid, rarely pleurotoid; pileus and stipe confluent; lamellae horizontal or descendant, white, more rarely pale orange or bluish gray or browish to purplish, otherwise pigment often confined to the lower portion of the stipe which is either ocher brownish to rufous, or cinereous to deep gray, fuscous, or bluish black, rarely very little pigment present even in the stipe but then the epicutis and the cheilocystidia both distinctly and constantly broom-like, lacerate; hymenophoral trama subirregular; hyphae

of the epicutis diverticulate, broom like, or at least cheilocystidia broom-like if the hyphae of the epicutis are smooth, but cystidia not necessarily present if the epicutis consists of lacerate hyphae.

Type species : M. ramealis (Bull. ex Fr.) Sing.

M. ramealis (Bull. ex Fr.) Sing. (Marasmius, Fr.); *M. anthocephalus* (Sacc.) Sing. (Marasmius, Sacc.); *M. semiustus* (Berk. & Curt.) Sing. (Marasmius, B. & C.); *M. opacus* (Berk. & Curt.) Sing. (Marasmius, Berk. & Curt.); *M. languidus* (Lasch) Sing. (Marasmius, Fr.); *M. pigmentatus* (Bliss) Sing. (Omphalia, Bliss); *M. purpureus* (Berk. & Curt) Murr. (Marasmius, B. & C.); *M. juniperinus* Murr.; *M. Trabutii* (R. Maire) Sing. (Marasmius, R. Maire); *M. caespitosus* (Pat.) Sing. (Clitocybe, Pat.); *M. tricolor* (A. & S. ex Fr.) Sing. (Omphalia, Gillet; Marasmius, Kühn.); *M. nigripes* (Schw.) Sing. (Marasmius, Fr.,; Heliomyces, Morgan; Marasmius subcinereus Berk. & Broome); also *Marasmius pandanicola* Henn., at least in the author's interpretation.

Sect. 5. **CALOPODES** Fr. (1838 ut sect. gen. *Marasmii*) (*Ramealinae* Kühn. p. p.). Characters same as in the preceding section but epicuticular hyphae and cheilocystia both non diverticulate.

Type species · Marasmius candidus (Bolt. ex) Fr.

M. albus-corticis (Secr.) Sing. [Agaricus albus corticis Secr.; Marasmius candidus (Bolt. ex) Fr.; Collybia, Sing. 1943, non Marasmiellus candidus (Bres.) Sing.].

Sect. 6. **PSEUDOCONIDIOPHORI** Sing. (1943 ut sect. *Hemimycenae*). Characters as in the preceding sections but epicuticular hyphae and cheilocystidia branched and the ends of the branches capitate and appearing conidia-like.

M. pseudoconidiophorus (Sing.) Sing. (Hemimycena, Sing. 1938).

Sect. 7 **FIBULAE** Sing. (1948) (*Aciculae* Kühn. p. p.). Habit decidedly omphalioid with soft, not tough stipe which is confluent with the pileus; lamellae arcuate and distinctly decurrent; pigments in all parts of the carpophore (microscopically) orange, but sometimes very scanty and sometimes accompanied by a blackish to bluish black pigment which is then localized at the umbilicus and the apex of the stipe; cystidia and dermatocystidia present, entire, not lacerate; hymenophoral trama subregular to subirregular (with a general axillar trend but not all hyphae running in the same direction); epicutis not made up of diverticulate hyphae. In deep moss.

Type species : M. fibula (Bull. ex Fr.) Sing.

M. fibula (Bull. ex Fr.) Sing. (Omphalia, Quél.; Mycena, Kühner);

M. setipes (Fr. sensu Ricken) Sing. (Omphalia, Ricken ; Mycena fibula var. Swartzii Kühn.).

Sect. 8. ADONIDI (Kühn. 1926 ut sectio em. Kühn. 1938 ut subsect. *Mycenae*) Sing. (1943 ut sect. *Hemimycenae*). Habit mycenoid to almost collybioid (rarely), with soft (neither tough nor fragile) stipe which is confluent with the pileus ; lamellae ascendant at first, rather narrow ; pigment bright colored (red, orange, pink, yellow) or rarely none at all ; (pleuro-and cheilo-) cystidia present ; cystidia with narrow tip ; hymenophoral trama regular to intermixed ; epicutis consisting of diverticulate hyphae ; conducting elements (oleiferous hyphae ?) usually abundant.

Type species : M. adonis (Bull. ex Fr.) Quél.

M. flavoalbus (Fr.) Sing. (Mycena, Quél. ; Hemimycena, Sing.) ; *M. floridulus* (Fr.) Sing. (Mycena, Karst. ; Collybia, Ricken) ; *M. adonis* (Bull. ex Fr.) Sing. (Mycena, Quél.) with numerous forms and varieties ; perhaps also *Mycena roseocandida* (Peck) Sacc., *Prunulus fusipes* Murr., and *Prunulus aurantiidiscus* Murr.

Sect. 9. FLOCCIPEDES (Kühn. 1938 ut sect. *Mycenae*). Habit collybioid, with soft (not tough) central stipe which is confluent with the pileus ; lamellae initially more or less ascendant, ventricose ; pigment dusky, dull-colored (fuscous, gray, melleous, yellowish brown) ; (pleuro-) cystidia and cheilocystidia present ; cystidia with broad neck ; hymenophoral trama very regular ; epicutis with smooth, elongate hyphae, often with dermatocystidia.

Type species : M. floccipes (Fr.) Sing.

M. floccipes (Fr. sensu Kauffm., Kühn.) Sing. (Collybia, Gillet, Mycena, Kühner ; Hemimycena, Sing. ; Mycena maura R. Maire ; Prunulus atribrunneus Murr.) ; *M. subalpina* (Hoehnel sensu Kühner) Sing. (Mycena, Hoehnel) ; possibly also *Collybia pseudoclusilis* Joss. & Konr. (but trama of stipe not metachromatic in clesyl blue mount).

Sect. 10. ACICULAE (1938 ut sect. *Mycenae*). Habit mycenoid, with soft, central, concolorous stipe which is distinct from the pileus (separated by a zone with small elements) ; lamellae initially more or less ascendant, adnate, or with descendant tooth, not ventricose ; pigment microscopically yellow, macroscopically orange ; cheilocystidia and (mostly) also (pleuro-) cystidia present ; trama subregular ; epicutis of the pileus consisting of diverticulate hyphae ; conducting elements none, or very few.

Type species : M. acicula (Schaeff. ex Fr.) Sing.

M. acicula (Schaeff. ex Fr.) Sing. (Mycena, Quél.) ; probably also

Mycena oregonensis A. H. Smith and *M. siskyouensis* A. H. Smith, both inserted here by Kühner.

Sect. 11. HIEMALES Konr. & Maubl. (1924-38 ut sectio *Mycenae*).

Habit mycenoid or almost omphalioid, with soft but not always fragile stipe which is more or less separated from the tissue of the pileus by a differentiated tissue-zone as in sect. *Aciculae*; lamellae ascendant, or horizontal at first, subfree to decurrent; pigment dusky, dull (gray, fuscous, melleous, blackish) rarely orange to pink or lacking (and then the stipe white at the apex in young specimens); (pleuro-) cystidia often present; cheilocystidia always present; epicutis consisting of diverticulate or (rarely) non diverticulate hyphae; conducting elements none or very few.

Type species : *M. hiemalis* (Osb. in Retz ex Fr. sensu Gillet) Sing.

Subsection Typici Kühn. (1938). Lamellae strongly ascendant when young.

Type species : as in the section.

M. rosipallens (Murr. sensu A. H. Smith) Sing. (Prunulus, Murr.); *M. leptophyllus* (Peck) Sing. (Mycena, Sacc.); *M. olidus* (Bres.) Sing. (Mycena, Bres.); *M. hiemalis* (Osb. in Retz ex Fr. sensu Gillet) Sing. (Mycena, Quél.).

Subsection Omphaliarii Kühn. (1938). Lamellae not strongly ascendant at first.

Type species : *Mycena speirea* (Fr.) Gillet sensu Kühner (non Fr.) (= *Marasmiellus camptophyllus* (Berk.) Sing.

M. camptophyllus (Berk.) Sing. [Omphalia, Sacc.; Mycena speirea (Fr.) Gillet sensu Kühner (non Fr.), nec Hoehnel; Omphalia, Cejp]; *M. atropapillatus* (Kühner & Mre.) Sing. (Mycena, Kühn. & Mre.); *M. phaeophyllus* (Kühn.) Sing. (Mycena, Kühn.); *M. Drepanocladi* (Sing.) Sing. (Hemimycena, Sing. 1943); *M. albus* (Bres.) Sing. (Omphalia, Bres.); *M. margaritifer* (R. Maire apud Kühn.) Sing. (Mycena, Mre.).

KEY TO THE SPECIES

The author refers to the published *Mycena* monographs which contain all the *Marasmielli* except sect. *Rameales* and sect. *Subrameales*. The latter sections can be determined with Kühner's *Marasmius* paper. The methodical determination of the tropical species is still impossible.

Kühner, R. *Le Genre* Mycena, Paris, 1938.

Kühner, R. *Nouvelles Recherches sur le Genre* Marasmius. *Ann. Soc. Linn. Lyon*, 79: 1-22. 1936.

47. MICROMPHALE Nees ex S. F. Gray

Nat. Arr. Brit. Pl. 1: 621. 1821, em. Sing. (non sensu Murr.)

Type species: *M. venosum* (Pers. ex) S. F. Gray [= *M. foetidum* (Sow. ex Fr.) Sing.]

Syn.: *Heliomyces* Lév. sensu Sing. (1936), R. Maire (1937) non sensu originali (see *Marasmius*).

Characters: Habit of the carpophores strictly marasmioid; pigment intercellular, incrusting the walls of certain hyphae; epicutis of the pileus (which is often striate or sulcate, often umbilicate, usually well-colored, thin) little differentiated, with smooth (but incrusted), filamentous, repent hyphae which are either parallel with each other or irregularly interwoven; often imbedded in a mucose mass together with the hyphae of the context, or else interrupted with air spaces; lamellae adnate to decurrent, subclose to distant; spore print white; spores hyaline, thin walled, smooth, nonamyloid, ellipsoid oblong or fusoid, or short-ellipsoid; cheilocystidia not very striking, basidiomorphous or in the shape of the basidioles (fusoid), if clavate, often with nodulose or ramosely appendiculate apices and their lower portions and the adjacent subhymenium incrusted by pigment; stipe deep fuscous black, or black, or somehow deep colored, pruinose or glabrous, insititious, central or rarely eccentric; black rhizomorphs sometimes well developed; context tough and reviving; trama nonamyloid, often partly gelatinized or with air-spaces between the strands of hyphae; all hyphae with clamp connections; odor usually fetid. On branches and logs, also on living organisms, sometimes forming endotrophic mycorrhiza with orchids.

Development of the carpophores: Unknown in detail.

Area: Almost cosmopolitan.

Limits: The gelatinous character of the context and cuticle is of somewhat irregular ocurrence in this genus. This genus is closest to *Marasmiellus* sect. *Rameales*, *Collybia*, and *Marasmius*, sect. *Androsacei*.

Marasmiellus, sect. *Rameales*: It differs from this section in the pigment, the odor, the more marasmioid habit (due to the darker tougher stipe). If there are no black rhizomorphs (which are never present in *Marasmiellus*), the cuticle or the whole sterile portion of the pileus is gelatinized.

Collybia : The fetid odor (somewhat of sauerkraut) and the smooth, repent epicuticular hyphae of *Micromphale* remind one of *Collybia* but this latter genus differs in the non insititious stipe, the absence of the central depression of the pileus, and the absence of either the black rhizomorphs or the gelatinous tissue in the cuticle or the trama.

Marasmius sect. *Androsacei* : This section differs from *Micromphale* in being quite dry (not gelatinized anywhere) and having constantly broom-like epicuticular elements (irregular in shape and diverticulate) whereas *Micromphale* has always smooth, filamentous hyphae in the corresponding layer. Aside from that, some species have demonstrably amyloid tissue whereas *Micromphale* has all tissues constantly nonamyloid.

In Fries' classification, the species of *Micromphale* are combined with *Marasmius* which is logical if the tougher species of *Collybia* are included as well as the section *Rameales* and *Subrameales* of *Marasmiellus*. The limits of the genus *Marasmius* in its old delimitation have never been clear, and some authors transferred many *Collybiae* to *Marasmius* and vice versa without any good reason at all. The reduction of *Marasmius* to a natural taxonomic unit and the erection of several smaller genera between *Marasmius* and *Mycena* on one hand, and *Marasmius* and *Collybia* on the other, on the basis of anatomical and chemical characters as proposed in successive papers since 1936 by the author, has increased the sharpness of determination and delimitation.

The genus *Heliomyces* is characterized in a way to suggest that it coincides with what we now call *Micromphale*. In fact, Singer, and later Maire decided in favor of the generic name *Heliomyces*, in order to avoid the creation of a new generic name. However, the typical species of *Heliomyces* in the original sense have all the anatomical and chemical characters of *Marasmius*, and it is rather doubtful whether they are actually gelatinous in fresh condition. As was pointed out by the editor of the *Annales d'Histoire Naturelle* when Levéillé published his genus, *Heliomyces* has no taxonomic value as an autonomous genus, and must fall into synonymy when treated according to the rules of the type concept. On the other hand, the genus *Micromphale* in the conception of S. F. Gray which is the valid post-Friesian presentation has as its largest single element the genus that is here called *Micromphale*, and it has therefore been proposed to emend it in this sense. This will avoid a nomen novum, and

at the same time dispose advantageously of the name *Micromphale*.

State of knowledge : The species of this genus have been studied very thoroughly by Kühner and this author. Aside from the five species indicated here, there are probably more, especially in the tropics. Further type studies on *Marasmii* will reveal under which name they have been described. The development of the carpophores is another item that is in need of special studies.

Practical importance : It is at present difficult to state whether or not *Micromphale* posseses practical importance. It is highly probable that the Horsehair disease of the rubber tree *(Hevea)* in Malaya is caused by a representative of this genus. But further taxonomic studies on this subject are necessary in order to make the generic position of this organism quite clear.

SPECIES

Sect. 1. RHIZOMORPHIGENA Sing. (1948). Characters much like those of the section *Rameales* of *Marasmiellus* but epicuticular hyphae (though strongly incrusted by the pigment) nearly non-diverticulate, irregularly interlaced, non gelatinized; stipe black, smooth and glabrous, in many cases directly continuing into black, branching, horsehair-like rhizomorphs; cheilocystidia nodulose or somewhat appendiculate branched at the apex, otherwise basidiomorphous; pileus often eccentric.

M. Westii (Murr.) Sing. *(Marasmius*, Murr.).

Sect. 2. PERFORANTIA Sing. (1948). Characters of the preceding section but stipe subpruinose or opaque, the black rhizomorphs little or not developed, the cuticle consisting of parallel, smooth, filamentous hyphae which are imbedded in a gelatinous mass; trama beneath it non gelatinous; cheilocystidia indistinct; pileus eccentric or more frequently centrally stipitate.

M. perforans (Hofm. ex Fr.) Sing. (Marasmius, Fr.; Heliomyces, Sing. 1943).

Sect. 3. GLOEONEMA (Kühn. ut sect. *Marasmii*, 1934). Characters of the preceding section but absolutely no rhizomorphs ever present; hyphae of the context likewise imbedded in a gelatinous mass.

Type species : M. foetidum (Sow. ex Fr.) Sing.

M. foetidum (Sow. ex Fr.) Sing. [Marasmius, Fr.; Heliomyces, Sing.; Micromphale venosum (Pers. ex) S. F. Gray]; *M. javanicum* Sing.; *M. saccharophilum* (Speg.) Sing. (Omphalia, Speg.).

KEY TO THE SPECIES

A. Cuticle non gelatinous and stipe glabrous and shining, often eccentric. Florida. *M. Westii*

A. Not combining these characters.

B. Context of the pileus non-gelatinous; on fallen needles of conifers in the temperate zone. *M. perforans*

B. Not combining these characters.

C. Spores narrow.

D. On wood, temperate species. *M. foetidum*

D. On *Saccharum officinarum* in the South American subtropics *M. saccharophilum*

C. Spores broad. *M. javanicum*

48. FLAMMULINA Karst.

Symb. Myc. Fenn. 30, *Meddel. Soc. Fauna Flora Fenn.* **18**: 62. 1891

Type species: Collybia velutipes (Curt. ex Fr.) Quél.

Syn.: Collybidium Earle, *Bull. N. Y. Bot. Gard.* **5**: 428. 1909.
Myxocollybia Sing., *Beih. Bot. Centralb.* Abt. B **56**: 162. 1936.

Characters: Habit collybioid; pigment usually present; pileus viscid, glabrous, with dermatocystidia; lamellae usually yellowish, rounded-adnexed or adnate-sinuate, moderately thin; spore print pure white; spores hyaline, smooth, nonamyloid; basidia normal; cystidia present on the sides of the lamellae; context fleshy in the pileus; hyphae nonamyloid, with clamp connections. On wood.

Development of the carpophores: Studied in detail by Moss (1923), considered as hemiangiocarpous.

Area: Temperate zones of all continents.

Limits: All authors agree about the necessity to separate this species from *Collybia*. What causes doubts is not the separation of this genus from other genera — it is almost isolated — but its position in the *Hemimyceneae*.

State of knowledge: The only species known, is completely described. It will be important, in future studies, to define the affinity with other genera more conclusively. If no other species of the *Hemimyceneae* has binucleate spores, and if this character on the other hand should be constant in *Flammulina*, it may lead to interesting conclusions as to the final position of *Flammulina*. On the basis of the known facts, *Flammulina* fits best between *Mi-*

nized cuticle, and *Macrocystidia*, another genus with dermatocystidia on the pileus, and pleurocystidia on the lamellae.

Practical importance: The type species is an excellent edible fungus, especially valuable since it forms its carpophores in winter when other mushrooms are rare. It may occasionally be a mild wound parasite.

SPECIES

F. velutipes (Curt. ex Fr.) Sing. (Collybia, Quél.; Pleurotus, Quél. 1886; Gymnopus, Murr.; Myxocollybia, Sing.).

49. MACROCYSTIDIA Heim.

Treb. Mus. Cienc. Nat. Barcelona **15**: 127. 1934

Type species: M. cucumis (Pers. ex Fr.) Heim

Syn.: *Macrocystis* Heim, *Le Genre* Inocybe, Paris, p. 71, 1931, non Agardh (1824).
Naucoria sect. *Macrocystis* Konr. & Maubl., *Icon. Sel. Fung.* **6**: 200, 1924-37.
Agaricus subgenus *Hypomnema* Britz., *Hym. Sudb.* 3 b, *Ber. Naturk. Ver. Augsburg* **27**: 196. 1883.

Characters: Habit of the carpophores collybioid or almost mycenoid; pigment present; pileus non viscid, glabrous, hygrophanous, campanulate with recurved margin; lamellae subfree, thin; spore print ocher-reddish (pink); spores pale stramineous pink under the microscope, smooth, attenuate toward the apex, ellipsoid oblong, with simple, slightly thickened wall, nonamyloid; uninucleate according to Kühner; basidia comparatively small, otherwise normal; cystidia voluminous, ventricose, at first subglobose, later elongate, thin-walled, hyaline; hymenophoral trama regular; cuticle consisting of repent filamentous hyphae with numerous large dermatocystidia forming a fragmentary epicutis; stipe central, rigid, but slender, without a pseudorrhiza, glabrous, beset with dermatocystidia; context colored, not tough in the pileus, without gelatinized portion; trama nonamyloid; hyphae with clamp connections. On herbaceous humus sticks, and wood.

Development of the carpophores: Unknown.

Area: Temperate and subtropical zone, especially in Europe and South America.

Limits: A rather isolated genus among all groups of agarics, but

with all the characters of this tribus and hardly related to any forms of the *Cortinariaceae* where it is sometimes placed.

State of knowledge : The two species described have been completely studied by Heim and the author. A third species remains unpublished up to the present date.

Practical importance : None.

SPECIES

M. cucumis (Pers. ex Fr.) Heim [Agaricus, Fr. ; Naucoria, Gillet ; Macrocystis, Heim ; Nolanea pisciodora (Cesati) Gillet ; Agaricus piceus Kalchbr.] ; *M. carneipes* (Speg.) Sing. (Omphalia, Speg.) ; *M. spec.* ined. (Argentina to Perú).

50. PHAEOMYCENA Heim

Rev. Mycol. **10** : 25. 1945 (1946), nom. subnud. ; *Bull. Soc. Myc. Fr.*, in print (?).

Type species : A. aureophylla Heim.

Characters : Habit of the carpophores collybioid ; well pigmented with a bright pigment, or little pigmented ; pileus subviscid or almost dry ; epicutis a thin layer of elongate, repent, smooth hyphae covering a hypodermium of vesiculose or swollen, fusoid, large hyphae, some of them with pigment bodies in their interior in dried material ; lamellae subsinuate subdecurrent or adnato-decurrent, intervenose and rather thick ; color of the spore print unknown ; spores under the microscope hyaline but with a stramineous endosporium (in NH_4OH), nonamyloid, thick-walled, not metachromatic in cresyl blue stains but the whole interior of the spore becoming deep blue by this dye, ellipsoid, with or without suprahilar depression, without germ pore, almost smooth but with an ornamentation like that of *Crepidotus*, sect. *Echinosporae,* i. e. heterogeneous in the outer layer of the wall and obscurely punctate when focussed at the upper surface, at least in *P. albidula* ; basidia somewhat thick-walled ; 4-spored ; cystidia none or (?) present ; hymenophoral trama consisting of an axillarly arranged, non-gelatinous melleous mediostratum and a very broad, strongly gelatinous hymenopodium (at least in *P. albidula*), all tramal hyphae thin to very thin, especially in the hymenopodium where

toward the basidia, slightly divergent at a nearly right angle in many cases; stipe central, solid to stuffed or somewhat hollow, with thickened base, consisting of thick-walled, intermixed hyphae; context of the pileus also with many thick walled hyphae, all hyphae nonamyloid. On wood or on the soil.

Development of the carpophores : Unknown.

Area : Tropics of America (Antilles) and Africa (Madagascar); perhaps in North America.

Limits : This genus is very well separated from all other genera of the *Tricholomataceae*, but somewhat ambiguous between that family and the *Crepidotaceae*. Microscopically, *Phaeomycena* is much closer to the latter family whereas macroscopically it is closer to the *Tricholomataceae*. Further evidence will probably decide on its final position in the classification. If the species described as *Mycena cineraria* A. H. Smith from Washington, U. S. A. belongs here, a relationship with *Fayodia* would be probable.

State of knowledge : The type species is better known macroscopically since a complete description has been made by R. Heim, *l. c.* The second species, *P. albidula* is better known microscopically. Both are in need of some additional information on the presence of clamp connections, chemical characters, exact color of the spore print, etc.

Practical importance : None.

SPECIES

P. aureophylla Heim; *P. albidula* (Pat.) Sing. (Collybia, Pat.); possibly *Mycena cineraria* A. H. Smith.

51. LACTOCOLLYBIA Sing.

Schweiz Zeitschr Pilzk. **17** : 16 (reprint-pagination). 1939.

Type species : *L. lacrimosa* (Heim) Sing.

Characters : Those of *Collybia*, but with very numerous and striking gloeovessels (Pl. XVIII, 3) and gloeo-cystidia (Pl. XXI, 3), or laticifers and pseudocystidioid prolongations of the latter; pigment mostly insignificant; stipe often eccentric and oblique; latex often present. On rotten wood and on living *Cycadineae*, also on living *Angiospermae*.

Development of the carpophores : Unknown.

Area : Tropical and subtropical, one species introduced in European greenhouses.

Limits : This genus is clearly delimited, not so much by its latex (which is present only in the type species) as by the abundance in conducting elements which are definitely of the gloeo type in two species. They are lacticiferous in the type species. *Lactocollybia* is on a much higher level than the genus *Collybia.* It has therefore been transferred to the *Hemimyceneae.* Among the genera of this tribus, the *Lactocollybiae* are closest to the genus *Marasmiellus* from which they differ in the anatomy of the cuticle, and the abundance of conducting elements which are not found in comparable forms among the *Marasmielli.* However, there are forms with rather prominent conducting elements among the latter genus, and some of the white species are close, in habit, to the non-lactescent white species of *Lactocollybia.*

State of knowledge : The type species is macroscopically well known, and enough is known about its microscopical characters to make its position in *Lactocollybia* certain. The other two species are completely known both macro- and microscopically.

Practical importance : The damage done to the hosts of the species growing parasitically on live *Cormophyta* is difficult to estimate. The cycads in the Botanical Garden in Leningrad where *L. cycadicola* occurs year after year, did not seem to be seriously injured.

SPECIES

Species with latex : *L. lacrimosa* (Heim) Sing. (Mycena, Heim).

Species without latex : on *Cycadineae : L. cycadicola* (Josserand) Sing. (Collybia, Josserand). On *Angiospermae . L. Angiospermarum* Sing.

Reduced series : 52. CYMATELLA Pat.

Bull. Soc. Myc. Fr. 15 : 193. 1899

Type species : C. marasmioides (B. & C.) Pat.

Characters : Habit cyphelloid (pezizoid); pileus glabrous, thin, with an epicutis of diverticulate hyphae in the manner of the *Marasmiellus,* sect. *Rameales* ; hymenophore none, hymenial surface smooth

lindric to obovate, medium sized (8 9 × 3 3.7 μ in the type species); stipe rather tough, variously attached to the pileus, thin and dark colored, not shining, insititious; trama of the pileus hyaline, consisting of hyphae which are thin-walled to moderately thin walled at places, running in parallel strands, often especially in the hypodermium, incrusted with a deep brown pigment, filamentous, clamped, nonamyloid. On rotting wood, twigs and dead ferns.

Development of the carpophores : Unknown.

Area : Antilles.

Limits : This genus comes close to *Marasmiellus*, sect. *Rameales* from which it differs in the complete absence of a hymenophore. The authentic material of *C. marasmioides* has no good spores (most are now collapsed) but the specimen is perfectly fertile; the type also shows an abundance of mature spores. Therefore, these species are not immature stages of lamellate forms. It is true that some species of *Marasmiellus* occur with smooth to venose hymenial surface but it appears that the hymenial surface of the *Rameales* is never quite smooth and this is the section that comes closest to *Cymatella*. Aside from that, *Cymatella*, also differs from *Marasmiellus* by the extremely small size of the carpophores (up to 2 mm in diameter). It is probably the best solution to consider *Cymatella* and *Marasmiellus* as closely related but generically different at least as long as no truly intermediate forms have been discovered.

State of knowledge : All three species have been studied by the author in addition to previous investigations by Patouillard and Burt. The genus has been divided into two sections, the first of which is called *Typicae* by Patouillard. The second is based on the genus *Discocyphella* Henn. in Warburg's *Monsunia* 1 : 43. 1900. No specimens are available for study of the type species of *Discocyphella*, *D. marasmioides* Henn. = *Cymatella Henningsii* Pat. Unless further studies prove Patouillard's and Hoehnel's (*Sitz.-ber. Ak. Wiss. Wien* **119** : 12. 1910) point that this species is congeneric with *Cymatella*, it must be disregarded.

Practical importance : Probably none.

SPECIES

C. minima Pat.; *C. marasmioides* (Berk. & Curt.) Pat. (Craterellus, B. & C.); *C. pulverulenta* (Berk. & Curt.) Pat. (Craterellus, B. & C.)

Reduced series : 53. **FLAGELLOSCYPHA** Donk

apud Sing., gen. nov. [44]

Type species : Cyphella minutissima Burt (= *Flagelloscypha minutissima* (Burt) Donk).

Characters : Habit of the carpophores cyphelloid (pezizoid), outside of the cup covered with hyaline, thick walled, thin, nonamyloid hairs which are incrusted with crystals of calcium oxalate (insoluble in acetic acid, soluble in HCl and HNO_3) ; spores hyaline, medium sized, cylindric, or amygdaliform, etc., nonamyloid ; basidia medium-sized, 4 spored ; cystidia none ; hyphae of the trama with clamp connections, nonamyloid ; subhymenium present but indistinctly delimited. On herbaceous stems and on the cortex of trees, on leaves, etc.

Development of the carpophores : Unknown in detail. Young dried specimens are a globose mass of hairs enveloping the hymenium.

Area : Probably nearly cosmopolitan.

Limits : This genus is sharply separated from all other cyphelloid genera by the characters of the hairs which according to the author's investigations, are chemically quite different from those of *Lachnella* and *Merismodes*. This refers it to this tribus where it seems to come closest to *Marasmiellus*. The latter genus contains a group of species (around *M. crispulus*) which has a tendency to produce mature hymenia on smooth or nearly smooth surfaces, and hairs on the sterile surfaces. These hairs are likewise nonamyloid. A further reduction of forms of this general type would perhaps lead to species like the *Flagelloscyphae*.

State of knowledge : The species immediately involved have been studied by Donk, Heim, Burt, and the author. The diagnosis given above is based on the type species and the data published by other authors on the additional species. The taxonomy of this group seems to be somewhat difficult (see Heim, *Treb. Mus. Ciènc. Nat. Barcelona* **15** : 56. 1934). It is not known whether these species are specific in regard to their habitat, but a certain degree of specificity may be expected.

Practical importance : Probably none.

[44] *Carpophoris cyphelloideis, crinibus dense tectis non amyloideis crystallis incrustatis, albis ; disco levi acystidiato ; sporis hyalinis, levibus, non-amyloideis, medio-*

SPECIES

F. minutissima (Burt) Donk (Cyphella, Burt); probably also *Cyphella punctiformis* (Fr.) Karst.; *Cyphella abieticola* Karst., and *Cyphella cruciformis* (Batsch ex) Fr., at least in the sense of Pilat (see *Bull. Soc. Myc. Fr.* **49**: 47, pl. VII, fig. 1 3. 1933).

Reduced series: 54 PHYSALACRIA Peck

Bull. Torr. Bot. Cl. **1**: 2. 1882.

Type species: P. inflata (Schw.) Peck

Syn.: Eoagaricus Krieger, *Md. Acad. Sc. Bull.* **3**: 8. 1923
Baumanniella Henn., *Engler's Bot. Jahrb.* **22**: 543. 1895 (sec. Corner)

Characters: Habit of the carpophores physalacrioid, i.e. the pileus is deformed to a globose or irregularly inflated, hollow club which is terminal on a short, thin, tough stipe, the latter not subject to negative geotropism; hymenium in irregular fragments but concentrated mostly in the areas of the pileus that are directed against the ground; sterile surfaces often made up by branched or diverticulate hyphae; pigment none, or yellow; spores hyaline, moderately large, ellipsoid to oblong or ovoid, smooth, thin walled, nonamyloid; basidia 4-spored, or 2-spored, chiastic (according to Baker's figures); basidioles fusoid or subfusoid, later clavate; pseudoparaphyses and cystidioles acute; metuloids not blue with cresyl blue, often incrusted, somewhat thick-walled, deep-rooted; subhymenium well developed; stipe consisting of somewhat thick walled, parallel hyphae which are elongate in the mature carphophore, with or without dermatocystidia; all hyphae and the elements of the hymenium as well as the covering layers of the sterile portions of the carpophore nonamyloid; hyphae with clamp connections. On dead and living plant tissue, most frequently on logs.

Development of the carpophores: Gymnocarpous (see McGuire, *Mycologia* **31**: 436. 1939, and Baker, *Bull. Torr. Bot. Cl.* **68**: 266-270, figs. 1-23. 1941).

Area: Tropical and temperate North America [11].

[11] One species, *P. tuba*, was reported from Spain by R. Heim (1934). This is evidently not a typical *Physalacria* but belongs to the *Clavariaceae*, in the neighborhood of *Clavaria pyxidata*. It is outstanding in being simple. This view is shared by M. A. Donk. This genus was subsequently published by Doty (*Lloydia* **10**: 38. 1947) who named it *Clavicorona*.

Limits : No difficulties can be foreseen in the delimitation of this genus.

State of knowledge : Some of the species have been studied by G. A. Baker *(l. c.)* and the author (ined.). These are indicated below.

P. inflata (Schw.) Peck ; *P. orinocensis* Pat. & Gaill. ; *P. Langloisii* Ellis & Everh. (P. aggregata Martin & Baker) ; *P. andina* (Pat. & Lagerh.) Pat. (P. orinocensis var. andina Pat. & Lagerh.) ; *P. tenera* Sydow ; *P. Sanctae-Martae* Martin & Baker apud G. E. Baker.

KEY TO THE SPECIES

For a key to the species of *Physalacria* see G. E. Baker, *l. c.*

Tribus MARASMIEAE Fayod

Prodrome, *Ann. Sc. Nat., Bot.* VII. 9. 340. 1889 (Marasmiés), em., Henn. in Engl. & Prantl, *Nat. Pfl.-fam.* 1** : 222. 1898.

Type genus : Marasmius Fr.

Syn. : Mycenés Fayod, *l. c.*, p. 310 ; *Myceneae*, R. Maire, *Publ. Junta Cienc. Nat. Barcelona*, p. 56. 1933.

Characters : Basidia normal, i. e. devoid of carminophilous granulosity ; habit of the carpophores usually mycenoid, mycenoid marasmioid, collybioid marasmioid, omphalioid, omphalioid marasmioid, or rarely more or less pleurotoid (but then the carpophores very small, thin, and with typical *Marasmius* stipes, or else — if astipitate — with pseudoamyloid epicuticular pilose covering), or reduced to cup-shaped (pezizoid) carpophores, or to stereoid (stipitate) carpophores ; epicutis of the pileus (in the cup shaped forms — outside layer of the cups) often containing pseudoamyloid or amyloid elements, or else it is a hymeniform layer from which long hairs or dermatocystidia arise, or else it is a monostratous or polystratous epithelium ; if the epicutis is not as just described, the trama of the pileus and or the spores are amyloid : trama rarely somewhat gelatinized, usually consisting of thick walled (and then context usually tough) or thinwalled (and then context usually fleshy-fragile) hyphae ; black rhizomorphs present or absent, if present — trama of the pileus amyloid ; hyphae usually with clamp connections, at least in the normal forms ; latex present or absent, if present, trama of the pileus amyloid. On a great

frequently on wood, foliage, dead herbaceous stems, on sand and humus, fern rhizomes, etc., also in deep moss, not parasitic on other fungi; sclerotia none.

Note: This tribus is the logical continuation of the tribus *Hemimyceneae*, and all genera are directly or indirectly related to the genus *Marasmiellus* or one of the allied genera. The main difference between this tribus and the preceding one is chemical, i. e. the species without any amyloid reaction anywhere belong to genera that are considered as part of the *Hemimyceneae*. However, there is a small number of exceptions. The author has not inserted in the *Hemimyceneae* three groups of species that, according to this definition actually should be put there. 1) the section *Alliati* of the genus *Marasmius* (and several isolated species of *Marasmius*); 2) the genus *Pseudohiatula* which is related to the *Marasmii* indicated under (1), and finally: 3) a few *Mycenae* which are closely related to species of *Mycena* with strong amyloid reaction, yet do not give this reaction, or a very weak one, in their spores and in the trama. In addition, a species without any hymenophore but otherwise very similar to the species of *Marasmius*, *Alliati*, in its anatomy as well as in its negative iodine reactions, is logically kept here instead of in the *Hemimycenae*.

KEY TO THE AGARICOID GENERA

A. Spores nonamyloid; carpophores reviving after they have dried out if remoistened in situ, epicutis consisting of a palisade or a hymenium of pseudoamyloid or amyloid hairs, or of diverticulate irregular elements, or of an epithelium; habit collybioid, marasmioid, or pleurotoid *Marasmiinae*, p. 397

B. Epicutis nonamyloid and also ordinarily not pseudoamyloid; trama amyloid or nonamyloid

C. Epicutis consisting of a hymeniform layer from which long hairs or dermatocystidia arise but pileus not pilose macroscopically; spores rather small, cystidia present, clamp connections often absent; trama nonamyloid. 55. *Pseudohiatula*, p. 318

C. Epicutis different. 56. *Marasmius*, p. 321

B. Epicutis pseudoamyloid or amyloid; trama nonamyloid.

D. Habit collybioid or marasmioid; stipe present (though sometimes eccentric); spores never pseudoamyloid; cystidia not pseudoamyloid 57. *Crinipellis*, p. 334

D. Habit decidedly pleurotoid; either spores (at least some of them) or cystidia pseudoamyloid 58. *Chaetocalathus*, p. 340

A. Spores amyloid, or else epicutis not as described above; habit never pleurotoid. *Myceninae*, p. 346

E. Spores nonamyloid, trama amyloid, pileus with an epicutis consisting of

smooth, hyaline, filamentous, repent hyphae, or of similar but diverticulate hyphae, or with some irregularly arranged dermatocystidia on the disc.

F. Pileus covered with a pellicle, or with a gelatinous layer; stipe also often covered with a pellicle, or else arising from a pedestal disc); epicutis of the pileus often made up of diverticulate hyphae (see *Mycena*)

F. Pileus not covered with a pellicle; pedestal (disc) none, hyphae of the epicutis smooth. 66. *Poromycena*, p. 363

E. Spores amyloid; trama amyloid or nonamyloid.

G. Trama amyloid, at least slightly so (never with smooth epicuticular hyphae and at the same time with nearly nonamyloid trama). 65. *Mycena*, p. 350

G. Trama nonamyloid

H. Hyphae of the epicutis repent, little branched, and smooth; dermatocystidia, hairs, or erect elements that form a palisade or hymenium absent; thick-walled hyphae of a velar layer also absent.

I. Lamellae very narrowly adnexed or subfree; spores minute and cylindric (not more than 5 μ long). 67. *Baeospora*, p. 366

I. Lamellae decurrent or at least broadly adnate, or else hymenophore not lamellate.

J. Hymenophore lamellate.

K. Pigment of the cuticle of the pileus dusky, dull colored (gray to black, umber, creamy-cinereous, etc.) or none; hyphae of the cuticle usually distinctly radial in arrangement; hyphae of the hymenophoral trama not incrusted with ferruginous brown pigment; stipe not strongly cartilaginous or tough as in *Marasmius*; spores usually short-ellipsoid to subglobose or globose, more rarely some more elongate spores present in a print together with short ones, with somewhat thickened more or less complex wall which is partly or entirely strongly amyloid; cystidia absent or present. 63. *Fayodia*, p. 347

K. Pigment rather bright colored; hyphae of the cuticle more or less radially arranged; hyphae of the hymenophoral trama with incrusting pigment; stipe strongly cartilaginous, or tough as in *Marasmius*, and often with a bright colored strigose tomentum at the base; spores ellipsoid to ellipsoid-oblong, always with thin, simple, smooth wall; cystidia always present on the sides of the lamellae but not always very conspicuous. 68. *Xeromphalina*, p. 367

J. Hymenophore poroid (if pileus lateral, see *Favolaschia*).

H. Hyphae of the epicutis not consisting of repent, little branched hyphae (or not exclusively so), or a velar layer consisting of thickwalled hyphae present, hymenophore lamellate, more rarely venose (if strongly poroid, see *Filoboletus*).

L. Elements of the epicutis narrow; carpophores reviving after having dried out and remoistened in situ; hyphae of the trama very thick-walled, at least many of them; habit of *Xeromphalina* or *Flammulina*. 69. *Heimiomyces*, p. 369

L. Elements of the epicutis broad, often balloon shaped, or narrow, and then pilose or with short branches; habit of *Omphalina* or *Mycena* or a small *Inocybe*, or one of the white, omphalioid *Marasmielli*; walls of the hyphae of the hymenophoral trama thin to very thin.

M. Velar layer (consisting of thick-walled hyphae) absent; hymenophore never venose.

N. Epicutis consisting of broad, often balloon-shaped elements, which are homologous with the cheilocystidia; they are more or less erect forming a hymeniform layer or a palisade, or fragments of such structures. 64. *Hydropus*, p. 349

N. Epicutis different.

O. Epicutis with long hairs; lamellae narrowly adnexed. (see *Leucoinocybe*, p. 373)

O. Epicutis different. (see *Mycena*)

M. Velar layer consisting of thick-walled hyphae present; hymenophore more or less venose; pigment none; trama very thin. 62. *Delicatula*, p. 346

KEY TO THE REDUCED GENERA

A. Habit of the carpophores marasmioid-stereoid 59 *Hymenogloea*, p. 342

A. Habit of the carpophores pezizoid.

B. Hairs well separated from the hypotrichial layer. 60 *Lachnella*, p. 343

B. Hairs not well separated from the hypotrichial layer, the lower portion of the hairs nonamyloid, the upper half slowly and slightly pseudoamyloid. 61. *Merismodes*, p. 345

Subtribus MARASMIINAE Sing.

Spores nonamyloid or somewhat pseudoamyloid; hyphae amyloid or nonamyloid; cystidia present or absent, if present — nonamyloid or pseudoamyloid; elements of the epicutis pseudamyloid or nonamyloid; epicutis never consisting of smooth, repent, hyaline, filamentous hyphae.

Note: The heterothallic strains of the *Marasmiinae* are ordinarily

clamped at the septa. Only the majority of the genus *Pseudohiatula* and one species of *Marasmius* are known to be constantly clampless.

The *Marasmiinae* consist of a normal agaricoid series, and a reduced series, just like the preceding tribus *Hemimyceneae*. The reduced genera are much like those of the *Hemimyceneae*, but no physalacrioid form has been observed. It is conceivable that the reduced forms indicated here are not the only ones in existence. The family *Cyphellaceae* is in need of a monographic treatment that will bring out those forms that are not aphyllophoraceous in their affinities but rather reduced forms of other groups, especially the *Agaricales*. The two cyphellaceous genera indicated here are especially remarkable for their hairs which are so strikingly similar to those of *Crinipellis* and *Chaetocalathus*.

Type genus: Marasmius Fr.

55. **PSEUDOHIATULA** (Sing.) Sing.

Notulae Crypt. e Sect. Crypt. Ac. Sc. U. S. S. R. **10-12**: 8. 1938

Type species: P. Cyatheae (Sing.) Sing.

Syn.: Mycena, Subg. *Pseudohiatula Beih. Bot. Centralbl.* **56** *Abt.* B: 165. 1936.

Characters: Habit of the carpophores mycenoid or collybioid; pileus non viscid, convex, without macroscopically visible hairs, but under a lens or under the microscope, hairs or dermatocystidia very conspicuous, projecting from among elements that form a hymeniform epicutis; pigment of the cuticle sepia to fuscous, yellowish-ocher-melleous, or none; hymenophore lamellate; lamellae not decurrent; spore print pure white; spores hyaline, smooth, nonamyloid, small, piriform, ellipsoid, subcylindric, or ovoid, thin walled; cystidia present on the sides and on the edges; hymenophoral trama regular or subregular; stipe thin and cartilaginous, somewhat tough in some specimens, often provided with a pseudorrhiza, beset with dermatocystidia; context of the pileus very thin, fleshy-soft when fresh; trama nonamyloid, consisting of hyphae without clamp connections in the temperate species, sometimes with clamp connections in the tropical species but even there the clamps very scattered. On living and dead *Pterodophyta*, on cones of conifers and on fallen fruits of *Magnolia*, also on decaying wood and bark of tropical trees.

Development of the carpophores: Unknown.

Area. Cosmopolitan as a genus, but the single species with smaller characteristic distribution.

Limits: The limits of this genus are easy to determine, and the group circumscribed by them is undoubtedly a natural unit. Yet, it has been claimed that these species are either part of older genera, or even part of sections of older genera. In the light of the chemical and anatomical characters of these species, their former insertion in *Mycena* or *Collybia* is now out of question. However, Kühner's suggestion — to consider them as belonging in the genus *Marasmius*, near section *Alliati*, — is worthy of consideration, because, undoubtedly, this is the group of agarics most closely related to the species of *Pseudohiatula*. There are, in the author's opinion, enough macroscopical, microscopical, and cytological characters to warrant a generic separation of these species. The anatomy of the cuticle of the pileus is sufficiently different in both genera to distinguish them sharply on this basis, and the appearance as well as the consistency is also sufficiently different to cause Fries, Ellis, Patouillard, and Singer to describe their species of *Pseudohiatula* not in *Marasmius* but in *Collybia*, or *Mycena* respectively. In fact, when studied in fresh condition, none of these species is really tough in the pileus but rather soft and in some cases so thin and transparent that they suggested *Hiatula* (to Lebedeva, 1922); none of the species of *Pseudohiatula* is able to revive when remoistened after drying out in situ. The substratum and the absence of clamp connections are also very specific in the temperate species of the genus which are the only ones that, by the habit and consistency — even though they are different from that of *Marasmius*, sect. *Alliati* — are at least comparable with *Marasmius*. On the other hand, the tropical species, are even less comparable with the *Marasmii* in the external characters. Summing up, we may say that the hiatus between *Pseudohiatula* and *Marasmius*, sect. *Alliati*, is sufficiently marked, and — unless truly intermediate species are discovered in the future — *Pseudohiatula* must be considered as generically autonomous.

Pseudohiatula differs from *Xerula* in the smaller spores, the absence of hairiness and furfuraceous floccose particles on the pileus; from *Oudemansiella* in the absence of mucous layers in the cuticle and in smaller spores. Undoubtedly, these two genera are also related to *Pseudohiatula* but its closer affinity with *Marasmius* sect. *Alliati* makes it advisable to refer the genus to the *Marasmieae* rather than to the *Hemimyceneae*.

State of knowledge: The species belonging in this genus are all well known; but perhaps more species will be discovered later. The tropical species do not seem to present any taxonomic difficulties at present, but the temperate species, in spite of repeated special studies, are still a difficult group.

Practical importance: The temperate species are all edible, and, where growing in large quantity, the pilei recommend themselves by a delicate flavor (though slightly bitter in very old caps) in soups, sauces, etc. They are especially valuable because of their unusual time of fruiting — winter and early spring when most other mushrooms are unavailable. It does not seem that the species on living *Cyathea* damages the plants attacked to an appreciable degree. Plants where the carpophores appeared in regular intervals were not visibly weaker than plants without fungus infection. It is quite possible that the fungus decomposes mainly dead material accumulating on the surface of the rhizomes.

SPECIES

P. Cyatheae (Sing.) Sing. (Mycena, Sing. 1936); *P. irrorata* (Pat.) Sing. (Collybia, Pat.); *P. conigenoides* (Ellis) Sing. (Collybia, Sacc.); *P. esculenta* (Wulfen apud Jacq. ex Fr.) Sing. (Collybia, Quél.; Marasmius, Karst.) consisting of ssp. *typica* (Sing. 1943); ssp. *Pini* (Sing. 1943) [= Marasmius conigenus (Fr. sensu Favre) Favre]; a third subspecies or autonomous species is known under the binomial *Marasmius tenacellus* (Pers. ex Fr.) Favre; *Mycena pubescens* (Murr.) Murr. seems to be very close to *P. irrorata* (Pat.) Sing.

KEY TO THE SPECIES

A. Cystidia and dermatocystidia broadly obtuse-rounded at the tip, often subcapitate and never acute, on various substrata.

B. Elements making up to the epicutis of the pileus, at least partly, or at least a large number of them, pigmented by a brownish intracellular pigment; the hairs among them 130-230 × 19-24 μ; on rhizomes of *Cyathea* in greenhouses. *P. Cyatheae*

B. Cuticle not as above; not on rhizomes of *Cyathea*.

C. Tropical species (Antilles); clamp connections sometimes present. *P. irrorata*.

C. Temperate to subtropical species or boreal species; clamp connec-

D. On « cones » of *Magnolia* ; temperate (warm) zone and subtropics in North America ; without pigment *P. conigenoides*

A. Cystidia and dermatocystidia rather acute, on pine cones (*Pinus silvestris*, *P. nigra*, *P. mugho*) in Europe (perhaps in North America and Northern Asia). *« Marasmius » tenacellus*

56. MARASMIUS Fr.

Gen. Hymen., p. 9. 1836

Type species : M. rotula (L. ex Fr.) Fr.

Syn.: *Heliomyces* Lév., *Ann. Sc. Nat.* III. **2**: 117. 1844 (type: *H. elegans* Lév.).

Androsaceus Pat., *Hymen. Eur.*, p. 105. 1887 [*Marasmius androsaceus* (L. ex Fr.) Fr.].

Chamaeceras Reb. ex O. Kuntze, *Rev. Gen. Pl.* **3²**: 454. 1898 [*Marasmius androsaceus* (L. ex Fr.) Fr.].

Mycenitis Earle, *Bull. N. Y. Bot. Gard.* **5**: 414. 1909 [*Marasmius alliaceus* (Jacq. ex Fr.) Fr.].

Scorteus Earle, *Bull. N. Y. Bot. Gard.* **5**: 415. 1909 [*Marasmius oreades* (Bolt. ex Fr.) Fr.].

Collybiopsis Schröter ex Earle, *Bull. N. Y. Bot. Gard.* **5**: 415. 1909 [*]

Marasmius sect. *Collybiopsis* Schröter in Cohn, *Crypt. Fl. Schles.* **3¹**: 559. 1889 [*Marasmius alliatus* Schaeff. ex Schröter].

Polymarasmius Murr., *N. Am. Flora* **9**: 286. 1915 (*Marasmius multiceps* Berk. & Curt.).

Characters: Habit marasmioid, i. e. collybioid or mycenoid, or almost omphalioid with tough, reviving consistency, especially in the stipe which is often dark colored and string like or horse hair like; epicutis of the pileus consisting of irregular (and then always diverticulate), or hymeniformly arranged elements or an epithelium, but among these elements no differentiated hairs or dermatocystidia projecting; the epicuticular elements not or slightly pseudoamyloid in very old carpophores; often, the upper extremity of the epicuticular elements beset with narrow appendages, which are erect like sterigmata and give these bodies a broom like appearance (broom-cells Pl. XII, 2);

[*] Earle indicates *Marasmius ramealis* as the type species of *Collybiopsis*. However, this genus is merely a new status of *Marasmius* sect. *Collybiopsis* Schroter. *M. ramealis* is then an ineptly chosen lectotype of the Schroterian section and the lectotype should be changed to *Marasmius alliatus* (Schaeff. ex Schröter) which is a synonym of *M. scorodonius* (Fr.) Fr. This change is necessary in order to make the type species comply with the diagnosis of both Schroter's and Earle's diagnoses, and also in order to keep the genus *Collybiopsis* from upsetting generic names in related groups (*Marasmiellus*, etc.).

XIII, 2); spores hyaline, thin walled, rather variable in size and shape, the shape variable within a single section (cylindric or ellipsoid spores being most common), and the size often very variable within a single species (especially in the species with large, narrow spores), smooth, from subglobose to clavate, ellipsoid or cylindric, or in the shape of the conidia of *Fusarium*, with simple, nonamyloid wall; basidia normal; cystidia or cheilocystidia or both usually present, the cystidia on the sides of the lamellae often thick-walled; basidioles fusoid; stipe cartilaginous tough or cartilaginous string like, or horse-hair-like, sometimes arising from black rhizomorphs (as in some *Micromphales*), attached to the substratum with rhizoid like fibrils, or small pseudorrhizas, or at least somewhat lacerate and fibrous at the base, or else insititious, without a disc at the base, and without latex when wounded; context often containing thick walled hyphae; all hyphae with clamp connections, amyloid or nonamyloid, if nonamyloid epicutis usually consisting of globose cells. On a wide variety of substrata, on sand, forest soil, on soil in fields, lawns, etc., on foliage or needles, on dead or living wood and other plant tissues, especially stems and grass roots, bamboo, etc.

Development of the carpophores: Hemiangiocarpous in at least several species.

Area: Cosmopolitan; more species are known from the tropics than from the temperate zones, and more in America than in Eurasia.

Limits: As for the limits of this genus, the reader is referred to the corresponding paragraphs in several other genera (*Marasmiellus, Pseudohiatula, Mycena, Crinipellis*).

State of knowledge: The European species have been studied carefully and systematically by R. Kühner who has contributed several valuable new characters (1934), anatomical as well as chemical. The author has studied 66 species, especially American and tropical forms, also some species from Central and Eastern Asia, Africa, etc., using all the criteria introduced by Kühner in order to find out whether or not these criteria would also hold for extra European material. It is reassuring to find that none of the type specimens examined from all these different regions tend to make Kühner's classification obsolete. They all fit well into the scheme as outlined by Kühner [**],

[**] Kühner's classification has been proposed without due regard to the conservation of published sectional names. The names proposed by him do not take advantage of the names already published as sectional names in the genus *Maras-*

and subsequently adopted by Konrad and Maublanc, and Singer. This classification (with some slight changes, mainly necessary in order to comply with the rules and recommendations of the International Rules of Nomenclature) is consequently considered as well tested and acceptable. This does not mean that the knowledge of the taxonomy of the genus *Marasmius* has progressed to the point where it is easy to determine the species. Naturally, the European species present the least difficulties at present. The North American and North Asiatic species follow. The South and Central American species are next, due to the large number of type specimens that could be restudied, and to the extensive collecting that has gone on in the West Indices and in Brazil. The species from Africa, East Asia and Malayasia, Australia and Polynesia are at present most difficult, and any effort in the direction of a monograph should take this situation into consideration with the aim of remedying it. The study of *Marasmius* requires much skill and patience in the observation of the anatomical data and the iodine reactions, yet the specimens can be preserved in a very satisfactory manner, and are usually plentiful. However, it is most important to gather material with notes on the colors since some of them are perishable on drying. Another inconvenience is the frequency of sterile material which is unique in this tribus and can only be compared with the situation in the *Lentineae*

mius. Fries divides the genus *Marasmius* in two subgenera, *Collybia* Fr. and *Mycena* Fr., and each of these is divided into sections. In order to preserve Kühner's names — which the author considers desirable — it must be assumed that lectotypes of the Friesian sections are admitted in the following manner:

Sect. *Scortei* Fr.: *M. urens* (which makes it a synonym of *Collybia*, sect. *Vestipedes* (Fr.) Quél.).

Sect. *Tergini* Fr.: *M. fuscopurpureus* (which makes it a synonoym of *Collybia*, sect. *Vestipedes*).

Sect. *Chordales* Fr.: *M. cauticinalis* (which makes it a synonym of the genus *Xeromphalina*).

Sect. *Rotulae* Fr.: *M. rotula* (which makes Kühner's *Rotulae* a homonym and synonym of the Friesian section).

It may be argued that the species with a similar name should be the type species in each of these sections. But this would not only create several sections incertae sedis (since they would be based on species incertae sedis), but it would also upset some of Kühner's sectional names which have been accepted by all modern authors. It is therefore in the spirit of the rules to make a few exceptions to the general principle of considering as lectotypes of the sections those species from which the sectional name is formed.

and *Schizophylleae,* and to a lesser degree in *Collybia.* The mature spores in younger specimens are often smaller than those in older specimens, or the size may depend on the weather conditions during the development of the carpophore. In other cases, constantly macrosporous and microsporous races can be distinguished within a single species. Unfortunately, nobody has thus far cared to devote a lifetime of these tiny organisms, so abundant in the tropical and subtropical forests.

Practical importance : Some species may have some importance in horticulture since they appear to be mycorrhizal partners of certain genera of orchids. Others have some importance as causing disease of tropical crops such as tea and sugar cane. However, the species determined and named in plant pathology. are not necessarily *Marasmii* in the modern sense but rather belong in *Marasmiellus* (*M. semiustus*) or *Crinipellis* (*C. perniciosa*), Some work has been done on the rôle played by *Marasmius oreades* on the pastures in Europe, America and Asia, and it appears that its influence on the growth rate and quality of the grass and other herbaceous vegatation is negative, i. e. its presence is undesirable in spite of the fact that the vegetation in immediate reach of the « fairy rings » appears to be better developed, deeper green (more nitrogen available) and faster growing than ordinarily. This same species is also a valuable edible mushroom of more than local significance since it is exceedingly common and well known under a number of vernacular names in several continents. *M. scorodonius* can be used for condiment (it has a garlic flavor), and some of the polypilous forms and these producing rhizomorphs, especially forms like *M. equicrinis* [29], have been used by the natives of the East Indies to tie jewelry.

SPECIES

Sect. 1. **ANDROSACEI** Kühn. (1933). Epicutis of the pileus consisting of irregular and irregularly arranged elements which are strongly diverticulate or broom-like ; stipe thin and seta like at least in its lower portion, reminding one of horse hair ; lamellae adnate to decurrent ; tissue of the stipe more or less amyloid in those species

[29] It is not quite clear whether the typical *M. equicrinis* belongs in the sect.

where the reaction can be observed (i. e. unless a strong pigmentation obscures the result of the test).

Type species : M. androsaceus (L. ex. Fr.) Fr.

M. albiceps Peck ; *M. androsaceus* (L. ex. Fr.) Fr. ; *M. splachnoides* Fr. ; *M. multiceps* Berk. & Curt.

Sect. 2. EPIPHYLLI Kühn. (1933 ut *Epiphylleae*). Epicutis of the pileus hymeniform, consisting of globose elements ; lamellae adnate to subdecurrent, not collariate, nor subfree ; cystidia prominent and constant ; stipe without rhizoids ; context amyloid or not ; pileus white or alutaceous ; carpophores usually very small, rarely reaching a diameter of 5-12 mm. Usually on leaves or stems.

Type species : M. epiphyllus (Pers. ex Fr.) Fr.

M. epiphyllus (Pers. ex Fr.) Fr. ; *M. epiphylloides* (Rea) Sacc. & Trott. (Androsaceus, Rea ; Androsaceus Hederae Kühn.) ; *M. epidryas* Kühn. ; *M. exfoliatus* (Kühn.) Kühn. (Androsaceus, Kühn. 1926) ; perhaps also *M. minutissimus* Peck.

Sect. 3. ALLIACEI Kühn. (1938 *ut Alliaceae*). Epicutis of the pileus made up by an epithelium or single layer of at least broad dermatocystidioid elements which are not pseudoamyloid ; trama definitely nonamyloid ; stipe not insititious ; elements of the epicutis constantly smooth.

Type species : M. alliaceus (Jacq. ex Fr.) Fr.

M. caucasicus Sing. ; *M. alliaceus* (Jacq. ex Fr.) Fr. ; *M. prasiosmus* (Fr.) Fr. ; *M. elongatipes* Peck ; *M. scorodonius* (Fr.) Fr. [M. alliatus (Schaeff. ex) Quél.] ; *M. chordalis* Fr. ; *M. platycystis* (Sing.) Sing. (Myxocollybia (?), Sing. 1943) ; *M. subalpinus* Sing. ; *M. alpinus* Sing. ; *M. hymenocephalus* (Speg.) Sing. (Collybia, Speg.).

Sect. 4. HYGROMETRICI Kühn. (1933 ut *Hygrometriceae*). Epicutis of the pileus hymeniform, its elements broom-like because of erect appendages (« broom cells ») ; trama definitely nonamyloid ; stipe central.

Type species : hygrometricus (Brig.) Sacc.

M. Leveilleanus (Berk.) Sing. (Heliomyces, Berk.) ; *M. Buxi* Fr. apud Quél. ; *M. Hudsonii* (Pers. ex) Fr. ; *M. corbariensis* (Roumeguere) Sing. [Agaricus, Roum. ; M. hygrometricus (Brig.) Sacc. ; M. olivetorum (Mont. & Fr.) Bres. in litt. ad Sacc. ; M. Oleae Quél.] ; *M. capillipes* Sacc. ; *M. rotalis* Berk. & Br. [M. rotula var. rotalis (B. & Br.) Bat. ; M. tenerrimus Wettst. non Berk. & Curt. ; M. Wettsteinii Sacc. & Sydow] ; *M. Ventallionii* Sing. ; *M. aciculiformis* Berk. & Curt. ; *M. Magnoliae* Sing.

Sect. 5. **APUS** Sacc. (1887), em. Same characters as sect. 4, but carpophores sessile, or almost. It is not quite certain whether any of the species in *Sylloge* **5** : 567 569 belong here.

M. Linderi Sing.; *M. sessilis* (Pat.) Sacc.

Sect. 6. **GLOBULARES** (1933 ut *Globularinae*). Same characters as in section 3 and 4, but tissue decidedly amyloid; elements of the epicutis smooth, or broom cells; stipe central.

Type species: M. Wynnei Berk. & Br. (*M. globularis* Fr. apud Quél.).

Subsect. **COLLINI** Sing. Elements of the epicutis of the pileus more or less globose or vesiculose and smooth.

Type species : M. collinus (Scop. ex Fr.) Sing.

M. setulosus (Murr.) Sing. (Gymnopus, Murr.); *M. torquescens* Quél.; *M. Plumieri* (Lév.) Sing. (Heliomyces, Lév.); *M. oreades* (Bolt. ex Fr.) Fr. [M. caryophylleus (Schaeff. ex) Schrot.]; *M. collinus* (Scop. ex Fr.) Sing. (Collybia, Quél.); *M. fissipes* (R. Maire) Sing. (Collybia, R. Maire); *M. lilacinus* (Coker) Sing. (Collybia, Coker); *M. major* Sing.; *M. ludovicianus* (Murr.) Sing. (Gymnopus, Murr.); *M. Todeae* Bres.; *M. tenuifolius* (Murr.) Sing. (Gymnopus, Murr.); *M. albipilatus* (Peck) (Collybia, Peck; Prunulus myceliosus Murr.); *M. albogriseus* (Peck) Sing. (Collybia, Peck; Collybia fimicola Earle); *M. synodicus* (Kunze apud Fr.) Fr. sensu Rick; *M. Wynnei* Berk. & Br. (M. globularis Fr. apud Quél.; M. carpathicus Kalchbr.); *M. strictipes* (Peck) Sing. Collybia, Peck); *M. fasciatus* Penn. (M. anomalus Peck non Lasch).

Note : Collybia arborescens Henn. which would key out in this subsection is made the type of an additional section of *Marasmius* (sect. *Sympodia* Heim 1948) by Heim who bases this unit on the compound stipe and the eventually bicellular (as in *Crinipellis mirabilis* Sing.) spores.

Subsect. **SICCINI** Sing. Elements of the epicutis — broom cells.

Type species : M. siccus (Schw.) Fr.

M. cohaerens (A. & S. ex Fr.) Quél [Mycena, Gill.; Marasmius ceratopus (Pers.) Quél.]; *M. echinatus* Theissen; *M. anomalus* Lasch apud Klotzsch in Rab. (M. litoralis Quél. & LeBreton; M. epodius Bres.); *M. atrorubens* Berk.; *M. helvolus* Berk.; *M. semipellucidus* Berk. & Br.; *M. rubroflavus* (Theissen) Sing. (M. nummularius var. rubroflavus, Theissen); *M. hinnuleus* Berk. & Curt.; *M. Balansae* Speg.; (? M. fulviceps Berk.; M. floridanus Murr.); *M. siccus* (Schw.) Fr. (M. campanulatus Peck; M. fulviceps Clem. non Berk.); *M. haema-*

Peck; *M. Berteroi* (Lév.) Murr. (Heliomyces, Lév.); *M. bahamensis* Murr.

Sect. 7. **PARAROTULAE** Sing. (1936). Characters as in the preceding section but lamellae obsoletely collariate and stipe insititious; elements of the epicutis smooth. On branches.

M. Rhododendri Sing.

Sect. 8. **ROTULAE** Fr. (1838). Elements of the epicutis of the pileus broom-cells; stipe insititious; lamellae usually collariate; tissue distinctly amyloid.

Type species : M. rotula (L. ex Fr.) Fr.

M. rotula (L. ex Fr.) Fr.; *M. ruforotula* Sing.; *M. limosus* Quél.; *M. Bulliardii* Quél. sensu Kühner [11]; *M. graminum* (Lib.) Fr.

KEY TO THE SPECIES

A. Epicutis not hymeniform; its elements diverticulate (broom-like).
B. Basidia 4-spored; all hyphae with clamp connections.
C. Stipe repent, branched; tropical America. *M. multiceps*
C. Stipe ascendant or erect; temperate species.
D. Stipe deep red-brown; lamellae rather close; in frondose woods. *M. splachnoides*
D. Stipe partly or entirely black in the lower part and hyaline at the apex, most frequently on needles of conifers.
E. Pileus white; context rather distinctly amyloid. North America. *M. albiceps*
E. Pileus not white; context nonamyloid in the pileus and very indistinctly amyloid in the stipe (indistinct reaction due to the strong pigmentation of the zones of the trama of the stipe that are usually amyloid in related species). Northern temperate zone. *M. androsaceus*
B. Basidia 2-spored; hyphae without clamp connections. *M.* sp. (on palms in Surinam)
A. Epicutis hymeniform.
F. Elements of the epicutis smooth.
G. Trama nonamyloid.
H. Small carpophores with white or stramineous pilei and insititious stipe; lamellae never free; projecting cystidia very conspicuous; on fallen leaves and on stems of various phanerogams.
I. Hyphae of the trama metachromatic in cresyl blue; on *Dryas octopetala* in European and Asiatic high mountain ranges. *M. epidryas*

[11] Kühner indicates that all *Rotulae* have amyloid hyphae; this implies that *M. Bulliardii* sensu Kühner has also amyloid hyphae, and excludes the possibility that *M. Bulliardii* Quél. might be interpreted as a synonym of a very similar species of the section *Hygrometrici*, viz. *M. rotalis* B. & Br.

I. Hyphae of the trama not metachromatic in cresyl blue; not on *Dryas*. Europe and Asia. *M. epiphyllus*

H. Medium sized to rather large, more rarely small carpophores with usually well colored, more rarely white piles and more or less deeply colored stipes which are not insititious but usually distinctly lacerate at the base from the rhizoid fibers; lamellae sometimes free; cystidia present or absent.

J. Pileus gray; stipe filamentous, black, shining, pruinose; in frondose woods of the Caucasus. *M. caucasicus*

J. Not combining these characters.

K. Odor of garlic present, or if it is lacking, the stipes red-brown and shining (in the majority of the species with odor, the stipe is either red brown and shining, or more pallid and more or less pruinose-tomentose, or black and opaque); in frondose woods, more rarely in coniferous woods.

L. Stipe cartilaginous, equal, pallid, subtomentose, or chordaceous (string-like), opaque and blackish to black, spores more than 7 μ long and more than 3.5 μ broad; odor of garlic present; only in frondose woods.

M. Spores very broadly ellipsoid; stipe chordaceous, blackish to black. *M. alliaceus*

M. Spores fusoid to cylindric; stipe not black *M. prasiosmus*

L. Stipe dark red brown, usually paler upwards and thickened at the apex, subchordaceous-subclavate. *M. scorodonius*

K. Odor none, or very slight and then not alliaceous; stipe deep brown to pallid, glabrous or pruinose, never distinctly shining; in coniferous woods; American species also in frondose woods.

N. In frondose woods in North America. Epicutis well developed; spores narrow (7 7-9 7 × 3 5-4 μ) or moderately narrow (6.5-7 × 4.3-4.5 μ).

O. Tropical forest; spores less than 7 7 μ long; lamellae strongly intervenose. *M. hymenocephalus*

O. Temperate and subtropical forest; spores 7.7 μ long or longer; lamellae not strongly intervenose. *M. elongatipes*

N. In coniferous woods and on grassy places near conifers and in the alpine or subalpine zone on meadows and tundras; epicutis either fragmentary, or spores broader, or confined to the alpine or montane zone of the mountains of Asia.

P. Epicutis of the pileus fragmentary; spores

P. Epicutis not fragmentary; cystidia not as described above; spores narrow or broad.

Q. Spores 8-10 × 6-7 μ on humus and detritus in coniferous woods of the temperate zone. *M. chordalis*

Q. Spores not exactly with the above measurements; growing in open places in the montane zone, also in the subalpine and alpine tundras.

R. Habit of the carpophores as in *Collybia maculata* but somewhat more slender. Altai. *M. subalpinus*

R. Habit of the carpophores as in *Collybia dryophila*; Caucasus. *M. alpinus*

G. Trama amyloid.

S. Stipe insititious on branchlets of *Rhododendron ferrugineum* in the subalpine zone of the Pyrenees, or on fragments of herbs and decaying leaves of *Quercus* in Europe; pileus always initially white, but later sometimes becoming brownish.

T. Spores 10-14.5 μ long, 4.7-5.7 μ broad; on leaves and stems. *M. exfoliatus*

T. Spores 9-10 × 2.3-4 μ, on branchlets of *Rhododendron ferrugineum*. *M. Rhododendri*

S. Stipe not insititious.

U. Setuloid dermatocystidia present on the pileus.

V. Lamellae adnate to a collarium; margin of the pileus undulate; in tropical America. *M. setulosus*

V. Lamellae free; margin of the pileus striate then sulcate; Europe, Caucasus and North Africa. *M. torquescens*

U. Setuloid dermatocystidia absent.

W. Spores more than 14 μ long. *M. Plumieri*

W. Spores up to 14 μ long.

X. Stipe solid or stuffed when mature.

Y. Spores 7.-10 × 4-5.8 μ; temperate species. *M. oreades*

Y. Spores 4-6 × 3-4 μ.

Z. Pileus 60-100 mm broad. Spain. *M. major*

Z. Pileus 10-15 mm broad. North America. *M. ludovicianus*

X. Stipe stuffed but soon becoming fistulose or hollow, cartilaginous.

AA. Pileus rufous-cinnamon; spores 8.3-8.7 (9) × 3.5-4.3 μ; lamellae rather crowded, rather narrow; on *Pteridophyta*. *M. Todeae*

AA. Not combining these characters.

BB. Spores 5-6 × 2.5-4 μ; cystidia on the sides of the lamellae and cheilocystidia both present; lamellae rather broad to very broad.

CC. Pileus 50-80 mm broad ; on leaves and leafmold. *M. tenuifolius*

CC. Pileus smaller ; on decaying wood and buried cones.

DD. Pileus 20-40 mm broad ; on decaying wood. (see « FF »)

DD. Pileus smaller

EE. On buried cones in North America. *M. albipilatus*

EE. On other decaying matter in South America. *M. synodicus*

BB. Spores larger, or cystidia absent, or lamellae narrow.

FF. Lamellae rather close, sometimes narrow ; North America.

GG. Spores 5-6 × 2.5-3 µ according to Pennington ; pileus reddish tan, later nearly white. *M. fasciatus*

GG. Spores larger ; pileus nearly white, later more colored, often with rusty-ochraceous places. *M. strictipes*

FF. Lamellae distant, or very distant, more rarely subdistant, broad.

HH. On meadows and open places among grass and herbs in temperate regions, especially in the mountains of Europe.

II. Pileus purplish-fuscous when wet, and not even slightly striolate, never campanulate and never umbonate. *M. fissipes*

II. Pileus less deeply colored when wet, striolate on the margin, initially campanulate, eventually umbonate. *M. collinus*

HH. In the woods on leaves, more rarely on wood or on dung, in temperate and subtropical zones.

JJ. Stipe abruptly divided into a hyaline upper and a richly colored lower portion ; on

JJ. Stipe not abruptly divided into two portions; in North and South America.

KK. Cystidia present on the sides of the lamellae becoming olive gray in Melzer's reagent. *M. lilacinus*

KK. Cystidia none. *M. albogriseus*

F. Elements of the epicutis not smooth, the epicutis consists of « broom-cells ».

LL. Trama of the carpophores nonamyloid or very slightly amyloid.

MM. Pileus centrally stipitate and not white; cystidia on the sides of the lamellae not conspicuous.

NN On needles of *Pinus pinea* and other Mediterranean pines; stipe green; Spain. *M. Ventallionii*

NN. On needles of conifers or on other substrata; stipe never green.

OO Very long, macroscopically visible spines on both the pileus and the stipe; on fallen leaves of *Ilex aquifolium*. *M. Hudsonii*

OO. Without long spines.

PP. Average length of spores smaller than 13 μ.

QQ. Lamellae with distinct collarium; pileus usually small, olive umber to umber with paler center, and often a small darker papilla in the central depression, on all kinds of leaves (including evergreens, grasses, needles, etc.) in Europe and Asia. *M. rotalis*

QQ. Not combining the above characters

RR. On wintergreen leaves, or at least on coarse thick leaves such as *Philyrea, Olea, Myrthus, Hedera, Magnolia*.

SS. Pileus pilose as in *Crinipellis*; on *Magnolia*, especially on the petioles. Florida. *M. Magnoliae*

SS. Pileus not pilose but glabrous; not on *Magnolia*.

TT. Pileus orange red; on *Nectandra*; Florida. *M. rufomarginatus*

TT. Pileus not orange red; not on *Nectandra*; in the Mediterranean region, most frequently on *Olea*. *M corbariensis*

RR. On tender leaves, or else on wood.

UU. Pileus very small, by far not reaching 10 mm.

VV. On fallen leaves such as *Syringa*, *Ulmus*, *Populus*, *Pirus*, in Europe. *M. capillipes*

VV. On wood in tropical forest.

WW. Spores and pileus small; cespitose in tropical America. *M. aciculiformis*

WW. Spores large. *M.* sp. ined.

UU. Pileus larger than 10 mm. in diameter. *M. Leveilleanus*

PP. Average length of spores about 13 μ; on *Buxus* in Europe. *M. Buxi*

MM. Pileus either pleurotoid or white; pleurocystidia conspicuous.

XX. Habit of the carpophores pleurotoid; on wood of trees in tropical Africa. *M. Lenderi.*

XX. Habit of the carpophores not pleurotoid; on fallen leaves in Europe. *M. epiphylloides*

LL. Trama of the carpophores amyloid.

YY. Stipe insititious, dark colored; lamellae attached to a collarium.

ZZ. Pileus whitish, frequently more than 8 mm. broad; widely distributed especially in temperate regions. *M. rotula*

ZZ. Pileus not all whitish, often very small.

AAA. Pileus reddish (orange rufous to Brazil red).

BBB. Broom-cells hyaline; on *Gramineae*; temperate species. *M. graminum*

BBB. Broom-cells entirely melleous; on wood in Florida. *M. ruforotula*

AAA. Pileus not reddish.

CCC. Lamellae 6-7; spores longer than 10 μ; on leaves and grasses. Europe. *M. limosus*

CCC. Lamellae 8-12; spores smaller than 10 μ; on leaves of various frondose trees and on needles and branchlets in Europe. *M. Bulliardii*

YY. Stipe not insititious (but the basal fibers often rather inconspicuous — use a lens); lamellae not attached to a collarium or not distinctly so.

DDD. Setuloid dermatocystidia present.

EEE. Medium sized carpophores with collybioid habit, widely distributed, especially in temperate zone. *M. cohaerens*

EEE. Small carpophores, found in southern Brazil. *M. echinatus*

DDD. Setuloid dermatocystidia absent.

FFF. Lamellae subporoid, directly adnate, intervenose,

GGG. Pileus small, reaching 20 mm but usually much smaller.

HHH. Pileus dark red to bright carmin red, purple.

III. Pileus dark red; all appendages of the broom-cells brown. *M. atrorubens*

III. Pileus lighter colored, or dark red but not all appendages of the broom-cells brown (dry material in ammonia).

JJJ. Pileus striped with white segments; some of the appendages or part of each appendage of the broom-cells brown; abundant red, soluble pigment also present. *M. tageticolor*

JJJ. Pileus not striped, and not pigmented as above.

KKK. All appendages of the broom-cells reddish; pileus deep red. *M.* sp. aff. *haematocephalus*

KKK. Part of the appendages of the broom-cells brownish; large part of the tropical belt, especially in the American tropics very common, rarely sporadically found farther north in North America. *M. haematocephalus*

HHH. Pileus some other color.

LLL. On grass and leaves of herbaceous plants, usually on *Gramineae*. *M. anomalus*

LLL. On leaves of trees and on logs

MMM. Fibrils of the base of the stipe or basal tomentum tawny-fulvous or deep melleous to brown.

NNN. Stipe pruinate; pileus smooth, cystidia indistinct; West Indies and Florida. *M. bahamensis*

NNN. Stipe shining, glabrous; pileus grooved; cystidia rather distinct. Tropical America. *M. hinnuleus*

MMM. Fibrils of the base of the stipe or basal tomentum either very inconspicuous or distinctly white.

OOO. Cystidia with very thick walls and sometimes projecting and conspicuous; tropical species.

PPP. Cystidia usually not lar-

ger than 25 × 7.7 μ; fibrils at the base of the stipe almost absent, very inconspicuous; apex of the stipe pellucid and hyaline. Asiatic species.
M. semipellucidus

PPP. Cystidia 36-52 × 8.5-10.5 μ; fibrils at the base of the stipe forming a rather conspicuous basal tomentum; apex not strikingly hyaline and pellucid; American species.
M. helvolus

OOO. Cystidia with very thick walls absent and cystidia generally not conspicuous (if this is a tropical species, see also « QQ »); American (temperate) species. *M. siccus*

GGG. Pileus comparatively large, at least several individual carpophores at a given locality reaching more than 20 mm of diameter when quite mature.

QQQ. Lamellae close to crowded.
(*M.* spp. from North America and Africa)

QQQ. Lamellae distant to almost subclose.

RRR. Pileus vinaceous to bay; lamellae subdistant *M. plicatulus*

RRR. Pileus tawny to ferruginous, richfulvous or deep cinnamon, sometimes tinged olive.

SSS. Lamellae distant; on leaves; spores 15.5-18.7 × 3.3-4.5 μ (see « HHH »).

SSS. Lamellae (distant to) subdistant to almost subclose; on leaves, or more often on decayed wood; spores usually between 8 and 10 μ long, rarely long. *M. Berteroi* and *M. Balansae*

57. CRINIPELLIS Pat.,

Journ. Bot. 3: 336. 1889, em. Earle, *Bull. N. Y. Bot. Gard.* 5: 414. 1909

Type species: *C. stipitaria* (Fr.) Pat.

Characters. Habit of the carpophores collybioid or marasmioid, rarely slightly pleurotoid; pileus and usually also stipe covered with thick walled elements which are usually distinctly hair-shaped (Pl. XXVIII, 1) and pseudoamyloid to almost amyloid, smooth, well sepa-

rated from the trama of pileus by a hypotrichial layer; hymenophore always well developed, lamellate; cheilocystidia present (Pl. XXVIII, 2, *c*, *g*); cystidia on the sides of the lamellae in one group of species frequent (Pl. XXVIII 2, *f*), not pseudoamyloid; spore print white or nearly so; spores (Pl. XXVIII, 3) hyaline, of various shapes, smooth, nonamyloid, thin-walled but after prolonged presence on the carpophore after maturity (without germinating) often becoming somewhat thick-walled, and in one species even septate (i. e. finally bicellular); basidia without carminophilous granulosity, 4 spored, more rarely some basidia in a specimen with less than 4 sterigmata, often more or less deformed (cystidioles, with all transitions to basidioles Pl. XXVIII, 2*a*); stipe central or eccentric, not reduced to a papilla; trama nonamyloid; hyphae with clamp connections. On dead and living plants, especially *Gramineae* and various trees and shrubs, usually on stems, roots, bamboo sticks, dead or living branches, fruits, etc.

Development of the carpophores : Unknown.

Area : Cosmopolitan.

Limits : This genus has been emended by Singer in 1943 so as to include all the *Marasmii* with pseudoamyloid epicutis, and nonamyloid trama and spores. On the other hand, the author excluded all the species without a true stipe. The species with pseudoamyloid hairs but without a true stipe have been transferred to *Chaetocalathus*. As a rule, the species of *Chaetocalathus* are characterized, aside from their shape, by either pseudoamyloid cystidia, or pseudoamyloid spores. The correlation of these characters is an evidence of a distinct hiatus between the two genera. *Crinipellis* differs from *Marasmius* in the presence of pseudoamyloid elements in the epicutis. The author has added to *Crinipellis* (sect. *Psilopus*) a species in which the epicutis does not consist of hair like elements (yet the elements are pseudoamyloid, even strongly so) and the stipe is smooth and glabrous. It is not impossible that there are other species of *Marasmius* that have more or less pseudoamyloid epicuticular elements but they would not be transferred to *Crinipellis* unless the trama were nonamyloid and broom cells were absent.

State of knowledge : The species of *Crinipellis* are comparatively well known. In a recent monograph, the author has admitted 29 species. Two more have been added since then. Four additional species are incompletely known.

Practical importance : Most species in *Crinipellis* are extremely

specific as far as host relations are concerned. In this category belongs *C. perniciosa* which is the fungus responsible for the witch-broom disease of cocoa which has done enormous damage in Surinam and adjacent regions.

SPECIES

Sect. 1. **PSILOPUS** Sing. (1942). Pileus with an epicutis of diverticulate, pseudoamyloid bodies (Pl. XXVIII, 1 *g*) but without actual hairs; stipe naked.

C. chrysochaetes (Berk. & Curt.) Sing.

Sect. 2. **EUCRINIPELLIS** Sing. (1942). Pileus with more or less elongate pseudoamyloid hairs (Pl. XXVIII, 1 *a-f*); stipe likewise pilose, never naked in all stages.

Type species: C. stipitaria (Fr.) Pat.

Subsect. Stipitarinae Sing. (1942). Cheilocystidia not differentiated from the cystidia — if there are cystidia at all; hairs not turning gray with KOH.

Type species: C. stipitaria (Fr.) Pat.

Stirps **Subtomentosa** (Hairs scattered, rather short, lamellae distant, spores large; cheilocystidia almost simple): *C. subtomentosa* (Peck) Sing.

Stirps **Zonata** (Pileus and stipe strongly hairy; spores small and broad, some of them decidedly pseudoamyloid; large carpophores growing on wood): *C. zonata* (Peck) Pat.

Stirps **Stipitaria** (Pileus and stipe strongly hairy; spores medium (between 7 and 10.5 μ); small species growing on *Gramineae*, more rarely on wood; pleurocystidia none): *C. septotricha* Sing.; *C. pseudostipitaria* Sing.; *C. bisulcata* (Pat. & Gaill.) Pat.; *C. stipitaria* (Fr.) Pat.; *C. atrobrunnea* Pat.

Stirps **Stupparia** (Pileus and stipe strongly hairy but disc typically smooth; spores broad (quotient 1.3-1.8); carpophores small, never on *Gramineae*): *C. Patouillardii* Sing.; *C. stupparia* (Berk. & Curt.) Sing.

Stirps **Carecomoeis** (Pileus and stipe strongly hairy; spores narrow and very long; carpophores small to very small; on leaves of trees and on small twigs): *C. carecomoeis* (Berk. & Curt.) Sing.

Stirps **Setipes** (Pileus and stipe strongly hairy but disc typically smooth, more rarely uniformly hairy; spores narrow — two to three times longer than broad — more rarely medium broad; carpophores small to large, never on bamboo or grass; cheilocystidia truly echi-

nate, rarely more inconstantly branched or forked): *C. hirticeps* (Peck) Sing.; *C. maxima* A. H. Smith & Walter; *C. campanella* (Peck) Sing.; *C. setipes* (Peck) Sing.; *C. Piceae* Sing.; *C. Dipterocarpi* Sing.

Subsect. Grisentinae Sing. (1942). Characters of subsect. *Stipitarinae* but hairs turning greenish gray in alkali, and spores at last appearing rectangular (Pl. XXVIII 3e) with a thin walled smaller upper cell and the wall of the lower cell (including the septum) thickened.

C. mirabilis Sing.

Subsect. Iopodinae Sing. (1942). Characters as in subsect. *Stipitarinae* but pileus bright colored (pink, red, lilac, violet, rubiginous when young and fresh); stipe sometimes short and curved but only exceptionally eccentric; hairs on the pileus and stipe not always long enough to show macroscopically.

Type species : C. iopus Sing.

C. rubiginosa Pat.; *C. rubida* Pat. & Heim; *C. Eggersii* Pat. apud Pat. & Lagerh.; *C. sublivida* Murr.; *C. iopus* Sing.; *C. perniciosa* (Stahel) Sing.; *C. Siparunae* Sing.

Subsect. Excentricae Sing. (1942). Pileus not brightly colored; stipe normally short, frequently more or less eccentric; cheilocystidia mostly much branched; center of the pileus darker than the margin; spores broad.

Type species : C. excentrica (Pat. & Gaill.) Pat.

C. perpusilla (Speg.) Sing. (Lentinus, Speg.; Crinipellis Bambusae Pat.); *C. excentrica* (Pat. & Gaill.) Pat.; possibly *C. Myrti* Pat. apud Pat. & Lagerh.

Subsect. Heteromorphinae Sing. (1942). Cystidia always present on the sides of the lamellae (Pl. XXVIII 2, f); the edge heteromorphous with a different kind of cystidia (cheilocystidia Pl. XXVIII, 2 g.; in most other respects like subsection *Stipitarinae*.

Type species : C. minutula (Henn.) Pat.

C. minutula (Henn.) Pat.; *C. trichialis* (Lév.) Pat.

KEY TO THE SPECIES

A. Species occurring in Europe.

B. On living trees in greenhouses (probably introduced from South America). *S. Siparunae.*

B. On *Gramineae* or on wood of *Syringa* *C. stipitaria.*

A. Species extra-European

C. Species ocurring in Africa.
  D. Madagascar. On humus and plant débris — *C. rubiginosa.*
  D. Continental Africa (North and West Africa).
    E. On *Gramineae.*
      F. Pileus 10-20 mm in diameter, grayish; lamellae distant; spores 9-11.8 (13) × 4.5-6 μ. — *C. subtomentosa.*
      F. Pileus 4-14 mm broad, never grayish; lamellae rarely distant; spores 7-10.8 × 4-8 μ.
        G. Species occurring in North Africa. — *C. stipitaria* (var. *graminealis*).
        G. Species occurring in tropical West Africa. — *C. pseudostipitaria.*
    E. On twigs; cheilocystidia different from the cystidia. — *C. minutula.*
C. Species occurring in Australia, America, Oceania, or Asia.
  H. Species occurring in the East Indies and in continental Asia.
    I. On *Gramineae* (in south-eastern Asia).
      J. Cheilocystidia different from the cystidia. — *C. trichialis.*
      J. Cheilocystidia not different from the cystidia (if the latter are present at all).
        K. Pileus light colored; spores rather broad; hairs mostly without close ladder-like septa. On grass. — *C. pseudostipitaria.*
        K. Not combining these characters.
          L. Spores about half as broad as long. — *C. atrobrunnea.*
          L. Spores very broad. — *C. sepiaria.*
    I. On wood or on leaves of trees.
      M. Stipe initially lilac, in Central Asia — *C. iopus.*
      M. Stipe not initially lilac.
        N. On wood. — *C. setipes* (var. ?).
        N. On leaves.
          O. On needles of spruce in Siberia. — *C. Piceae.*
          O. On leaves and fruits of *Dipterocarpus.* — *C. Dipterocarpi.*
  H. Species occurring elsewhere.
    P. Species occurring in Tropical America (not on the North American continent) including Bermuda.
      Q. Species growing on parts of herbaceous plants, also on *Bambusa.*
        R. Spores less than twice as long than broad. — *C. perpusilla* (on *Bambusa*). *C. atrobrunnea* (on grass).
        R. Spores twice as long as broad or more
          R*. Pileus tomentose. — *C. subtomentosa.*
          R*. Pileus hairy. — *C. bisulcata, C. pseudostipitaria.*

T. Stipe naked. *C. chrysochaetes.*

T. Stipe pilose

U. Lamellae broad; spores larger than 10 μ. *C. carecomoeis.*

U. Lamellae narrow; spores smaller than 10 μ. *C. stupparia.*

S. On decayed wood, or on living branches of trees, or on fallen diseased parts of *Theobroma.*

V. On decayed wood.

W. Pileus bright pink. *C. rubida.*

W. Not so.

Y. Pileus with lilac shades or sublivid.

Z. Spores 5-6.3 μ broad. *C. Eggersii.*

Z. Spores 3.5-5 μ broad. *C. sublivida.*

Y. Pileus not so colored.

AA. Stipe short, eccentric. *C. excentrica.*

AA. Stipe not so.

BB. Spores twice as long as broad, or broader.

CC. Cheilocystidia echinate. *C. stupparia.*

CC. Cheilocystidia simple or scarcely branched. *C. Patouillardii.*

BB. Spores narrower. *C. septotricha.*

V. On living trees (in the branches) or on freshly fallen parts of them, destroyed by their action (« krulloten » pods of *Theobroma*).

DD. Pileus crimson red; on *Theobroma.* *C. perniciosa.*

DD. Pileus lilac to brownish lilaceous. On *Siparuna.* *C. Siparunae.*

P. Species occurring outside Tropical America.

EE. Species occurring in North America (excluding the Caribbean Islands).

FF. On *Gramineae.*

GG. Pileus 6-13 mm; lamellae not distant. *C. stipitaria* var. *graminealis.*

GG. Pileus 12-24 mm; lamellae distant. *C. subtomentosa.*

FF. Not on *Gramineae.*

HH. On fallen needles of spruce. Western North America. *C. Piceae.*

HH. On wood.

II. Pileus broader than 12 mm, disc not naked and glabrous.

JJ. Spores small to medium, never pseudoamyloid, about twice as long as broad, or more.

KK. Cheilocystidia 35-100 × 7-14 μ, entire. *C. maxima.*

KK. Cheilocystidia branched. *C. hirticeps.*

JJ. Spores small, some of them pseudoamyloid, less than two times longer than broad. *C. zonata.*

II. Pileus small (less than 13 mm broad), or, if larger, with a smooth umbilicus or a smooth disc in the center.

LL. Pileus campanulate with a fulvous tawny tinge; cheilocystidia forked and branched but not echinate. *C. campanella.*

LL. Pileus convex-expanded; cheilocystidia echinate, at least in their majority. *C. setipes.*

EE. Species occurring elsewhere (mostly on Pacific islands).

MM. Hairs turning greenish gray in KOH; pileus dark reddish brown. *C. mirabilis.*

MM Hairs not so reacting; pileus not so colored

NN. Spores more than 10 μ long, narrow. *C. carecomoeis*

NN. Spores up to 10 μ long *C. Patouillardii.*

58. CHAETOCALATHUS Sing.

Lilloa **8**: 518. 1942

Type species: *C. craterellus* (Dur. & Lév.) Sing.

Characters: Habit pleurotoid (Pl. XXVIII, 4 *a, f*); pileus pilose with thick walled, smooth pseudoamyloid to almost amyloid hairs (Pl. XXVIII, 4 *b, i*) which are very long and distinctly separated from the trama of the pileus by a hypotrichial layer; hymenophore well developed, lamellate; spores (Pl. XXVIII, 3 *h-i*) hyaline, thin-walled, eventually sometimes becoming somewhat thick walled, smooth, nonamyloid or pseudoamyloid; basidia (Pl. XXVIII, 4) without carminophilous granulosity, 4 spored, or more rarely with an inconstant, lower number of sterigmata; cheilocystidia always present, cystidia on the sides of the lamellae (Pl. XXVIII, 4 *d, e, g, h*) also often present and either entire (then strongly incrusted by a crystalline incrustation) or variously forked or divided, very frequent-

ly pseudoamyloid; stipe (Pl. XXVIII, 4 *a*) rudimentary or more rarely absent, never directly attached to the substratum (since it has lost its function — the pileus itself being attached to the substratum); trama nonamyloid; hyphae with numerous clamp connections. On wood, bamboo, leaves, bark, sticks and stems, etc.

Development of the carpophores : J. de Seynes has given some data on the development of *C. craterellus* (*Ann. Soc. Linn. Maine et Loire* **11**: 1-10. 1869); no recent studies on the details have been published.

Area : Cosmopolitan, predominantly tropical.

Limits : Species with the stipe reduced to a button which is not attached to the substratum, are not found in *Crinipellis*, and a combination of pleurotoid habit and either pseudoamyloid cystidia or pseudoamyloid spores is also not found in that genus. These characters determine *Chaetocalathus* as natural genus, clearly different from *Crinipellis*. The presence of a hymenophore distinguishes *Chaetocalathus* from the reduced forms such as *Lachnella* and *Merismodes*.

State of knowledge : The species of this genus are well known. They have been monographed by the author, together with *Crinipellis*, in *Lilloa* **8**: 441-534. 1942. Eleven species are admitted.

Practical importance : None, as far as known at present.

SPECIES

Sect. **1. OLIGOCYSTIS** Sing. (1942). Pseudoamyloid, sterile bodies in the hymenium mostly absent, or if there are any, they are accompanied by numerous nonamyloid or even more or less thin-walled cystidia; spores (with few exceptions) pseudoamyloid.

Type species : C. craterellus (Dur. & Lév.) Sing.

C. craterellus (Dur. & Lév.) Sing. *C. fragilis* (Pat.) Sing.; *C. niduliformis* (Murr.) Sing.

Sect. 2. **MERISTOCYSTIS** Sing. (1942). Pseudoamyloid, sterile, thick walled bodies in the hymenium constantly present, usually crowded near and at the edges of the lamellae, forked or distinctly divided, not or little incrusted. Species of the Eastern Hemisphere.

Type species : C. africanus (Pat.) Sing.

C. pachytrichus Sing.; *C. bicolor* (Pat. & Demange) Sing.; *C. congoanus* (Pat.) Sing.; *C. africanus* (Pat.) Sing.

Sect. 3. **HOLOCYSTIS** Singer (1942). Cystidia with very thick wall which is strongly incrusted by crystals and strongly pseudoamyloid; these cystidia are not branched or nearly entire,

almost equally distributed on the sides and edges of the lamellae.

Type species : C. carnelioruber Sing.

C. carnelioruber Sing. ; *C. liliputianus* (Mont.) Sing. ; *C. galeatus* (Berk. & Curt.) Sing. ; *C. asperifolius* (Pat.) Sing.

KEY TO THE SPECIES

A. Characters of section *Oligocystis* (see above).
  B. Pseudoamyloid cystidia completely lacking
    C. Stipe rudiment distinct ; Europe and Africa. *C. craterellus*
    C. Stipe rudiment indistinct or absent ; Asia. *C. fragilis*
  B. Pseudoamyloid cystidia present ; America. *C. niduliformis*
A. Characters different from those of section *Oligocystis*
  D. Asiatic and African species.
    E. Cystidia simple, entire. *C. galeatus*
    E. Cystidia branched, forked or somehow divided
      F. Stipe rudiment white ; Tropical Asia
        G. Hairs 5,5-12 μ thick ; Philippines. *C. pachytrichus*
        G. Hairs thinner ; Tonkin. *C. bicolor*
      F. Stipe rudiment colored, or none ; Tropical Africa
        H. Edge of the lamellae heteromorphous from 18-29 μ long cystidia. *C. congoanus*
        H. Edge of the lamellae with 25-47 μ long cystidia, i. e. the same type that is also found on the side of the lamellae. *C. africanus*
  D. American species.
    I. Pileus red. *C. carnelioruber*
    I. Pileus not red
      J. Spores 7 × 4,5 μ ; on wood of *Juniperus* (see *C. niduliformis*)
      J. Spores mostly larger ; not on wood of *Juniperus*.
        K. Spores 5-7,7 μ broad ; not on bark of living *Murraya*.
          L. Cystidia 31-51 × 7,7-12 μ. *C. liliputianus*
          L. Cystidia larger. *C. galeatus*
        K. Spores 5-5,5 μ broad ; on bark of living *Murraya*. *C. asperiformis*

Reduced series 59. HYMENOGLOEA Pat.

Ess. taxon., p. 146. 1900.

Type species : H. Riofrioi Pat.

Syn. : Libellus Lloyd, *Myc. Writ.*, *Letters* 45, p. 6 1913 (type *Craterellus papyraceus* B. & C.).

Characters : Habit marasmioid stereoid, i. e. reminding one of the large tropical stipitate *Sterea*, and at the same time of a large representative of the genus *Marasmius*, without hymenophore, but with

well developed central stipe. It has otherwise all the characters of sect. *Alliati* of *Marasmius*.

Development of the carpophores : Unknown.

Area : Tropical America.

Limits : The genus is well separated from all other genera of the *Marasmieae* except for *Marasmius* itself. The only known character that separates it from *Marasmius* is the smoothness of the hymenial surface, a character that is unknown in the section *Alliati* but does occur in the closely related section *Epiphylli*. However, the species of the section *Epiphylli* are fungi of a quite different type, in size, pigmentation and partly in chemical characters. On the other hand, it may not be coincidental that all specimens yet seen of *Hymenogloea* were sterile. If it should turn out that *Hymenogloea* is merely a juvenile stage of some unknown (or known?) large species of *Marasmius*, it would of course become necessary to abandon *Hymenogloea* as a separate genus. It is, however, admitted here on a temporary basis.

State of knowledge : Hymenogloea papyracea, the only species known, has been studied thoroughly by the author, but the spore characters and data on the development of the carpophores are still wanting.

Practical importance : Probably none.

SPECIES

H. papyracea (Berk. & Curt.) Sing. (Craterellus, B. & C.; Libellus, Lloyd; Stereum Rtofrioi Pat.; Hymenogloea, Pat. 1900).

Reduced series 60. LACHNELLA Fr.

Corp. Flor. Prov. I. Floram Scanicam, p. 343. 1836.

Type species : Peziza albo-violascens A. & S. ex Fr. [illegible].

Characters : Habit of the carpophores cyphelloid, small, gregarious; pileus reduced to a cup-shaped organ which is directly (without

[illegible] According to J. A. Nannfeld in *Nova Acta Soc. Sc. Upsal.* IV 8 (2): 260. 1932, *Lachnella* in the sense of Boudier (who neglected the fact that the type species is undoubtedly a Basidiomycete) is a synonym of *Lachnum* (Retz.) Karst. With the name *Lachnum*, in addition to many others, available for the *Discomycetes*, it can hardly be expected that the generic name *Lachnella* will be conserved for the ascomycetous forms introduced in the genus *Lachnella*. Consequently, the author feels safe to apply the generic name *Lachnella* according to the provisions of the International Rules, i. e. for the basidiomycetous group treated below.

a stipe) attached to the substratum; sterile outside of the cup formed by hairs which are long, thick-walled, entirely slightly to strongly pseudoamyloid, well differentiated from the tramal hyphae from which they are separated by a septum, thus very similar to the hairs of the genera *Crinipellis* and *Chaetocalathus* but not smooth but finely echinulate over most of their surface, the echinulation not distinctly pseudoamyloid; spores hyaline, large and broad, attenuate at the apex, without a distinct suprahilar depression but sometimes with a depression higher up on the inner side of the spore and consequently often slightly curved, thin walled, smooth, very rarely assuming a central septum before discharge, nonamyloid, axillarly asymmetric (i. e. heterotropic); basidioles more or less fusoid (*Collybia-Marasmius* type); cystidia none or inconspicuos; subhymenium either strongly enlarged, forming a deep layer (and then the basidia unusually long), or reduced to a monostratous layer of branched hyphae which is extremely thin and very inconspicuous (and then the basidia shorter and ascendant); margin of the cups gradually becoming sterile, with short echinulate hairs taking the place of the basidia; stipe none, not even a rudiment present, but a pseudostipe which is dorsal-central or dorsal-eccentric, often present; tissue nonamyloid, rather thin to very thin; all hyphae with clamp connections, most of them thin walled, some slightly thick-walled. On dead sticks and branches, trunks, cortex, etc.

Development of the carpophores: The disc of dried material is initially covered by recurved hairs above the hymenial layer, later opening by expansion of the margin; methodical development studies have not been made recently.

Area: Cosmopolitan.

Limits: The limits of this genus against the other marasmioid genera do not present any difficulties. It is obvious that *Lachnella* is closest to *Chaetocalathus* which differs in the well developed hymenophore and the smooth epicuticular hairs; also in the presence of pseudoamyloid cystidia or spores. *Merismodes* differs clearly in the characters of the hairs which are not sharply separated from the underlying tissue, and in the different type of spores. A similar type of echinulate hairs is not found in the whole *Marasmiinae*-series but can be recognized in the cortical hairs of such Mycenas as *Mycena osmundicola*. However, the latter has amyloid spores, a central, long stipe, and well developed hymenophore. It must be assumed that

series of *Marasmieae* which has probably originated somewhere between *Marasmius* and *Crinipellis-Chaetocalathus.*

State of knowledge : The smallness of the specimens and the difficulty of determination of the *Cyphellaceae* (in whatever sense this word may be understood) may have prevented a more detailed knowledge of the forms which will eventually enter this genus. At present, we know only three species which the author has studied personally, and which are treated here according to an oral suggestion by M. A. Donk.

Practical importance : Hardly any.

SPECIES

L. alboviolascens (A. & S.) Fr. (Cyphella, Karst.); *L. villosa* (Pers. ex Fr.) Donk apud Sing. (Peziza, A. & S. ex Fr.; Cyphella, Karst.); *L. Tiliae* (Peck) Donk apud Sing. (Peziza. Peck; Cyphella, Cooke).

Reduced serie 61. **MERISMODES** Earle

Bull. N. Y. Bot. Gard. 5 : 406. 1909

Type species : *Cantharellus fasciculatus* Schw.

Characters : Same as in the preceding genus but with smaller and very narrow, spores which have a suprahilar applanation; hairs either hyaline or colored (at least in alkali), very slightly pseudoamyloid, reacting with Melzer's reagent rather weakly (but definitely) in the upper half whereas the lower half is almost nonamyloid and indistinctly separated from the underlying hyphae; the very apex of the hairs is nonamyloid in most cases; subhymenium always rather indistinct. On sticks, cortex, wood, etc.

Development of the carpophores : Probably same as in *Lachnella.*

Area : Cosmopolitan.

Limits : See *Lachnella.*

State of knowledge : As in *Lachnella.* Only one species is known.

Practical importance : None.

SPECIES

M. fasciculata (Schw.) Donk apud Sing. (Cantharellus, Schw.; Cyphella, Berk. & Curt.).

Subtribus MYCENINAE Sing.

Spores amyloid, or rarely nonamyloid; hyphae amyloid or nonamyloid; cystidia present or absent, if present, nonamyloid; epicutis never pseudoamyloid consisting of smooth, repent, hyaline filamentous hyphae, or having some other structure; hyphae of the trama with clamp connections in all normal (heterothallic) forms.

Type genus: Mycena (Pers. ex Fr.) S. F. Gray.

62. DELICATULA Fayod

Prodrome, *Ann. Sc. Nat.*, VII, 9: 313, 1889

Characters: Habit of the carpophores mycenoid-omphalioid, small and slender, almost transparent, hygrophanous, pigmentless; pileus at first with a velar layer consisting of thick-walled hyphae; epicutis — a thin layer of thin-walled, filamentous, repent hyphae; hypodermium made up of somewhat thicker, radially arranged hyphae and proliferating beyond the margin of the pileus forming thin filamentous appendages; hymenophore often reduced to mere veins (especially in immature or retarded specimens), otherwise consisting of narrow lamellae; spores hyaline, subamygdaliform-ventricose, smooth, amyloid, with thin homogeneous wall; basidia normal; cystidia none; hyphae of the trama nonamyloid, subregularly arranged in the hymenophore, with numerous clamp connections. On débris and sticks, logs, etc.

Development of the carpophores: Hemiangiocarpous (see Kühner, *Contrib. Bas.*, p. 96, 1926).

Area: Unknown, probably temperate.

Limits: This genus differs from all other genera by its veil, the amyloid spores, the hemiangiocarpous development of the carpophores and the structure of the cuticle of the primordia, also by the lack of all kinds of pigment. It has the appearance of *Marasmiellus*, sect. *Candidi* but can be distinguished easily by the amyloid spores.

State of knowledge: Only one species has been studied thoroughly (Kühner, Josserand, Singer), but there may be more.

SPECIES

D. integrella (Pers. ex Fr.) Pat. (Omphalia, Quél. sensu Fayod; Delicatula bagnolensis Gilbert); according to R. Maire also *D. cuspidata* (Quél.) Cejp; according to Cejp several species, some of them also indicated by Fayod and Patouillard, but they are insufficiently known, and may perhaps belong to *Marasmiellus*.

63. FAYODIA Kühner

Bull. Soc. Linn. Lyon 9: 68 1930, emend Sing *Rev Myc* 1: 279 1936.

Type species: Omphalia striaepilea sensu Ricken.

Characters: Habit of the carpophores collybioid, omphalioid or clitocyboid; pigment dark, dusky and dull (gray, umber, sepia-fuscous to nearly blackish), or more rarely without any pigment; pileus with an epicutis consisting of smooth and repent hyphae, rarely some scattered hair-like hyphal ends ascendant or erect, and projecting beyond the general level of the epicutis; lamellae subfree, adnexed-sinuate, adnate or adnate-subdecurrent, also often frankly decurrent; spores hyaline, short-ellipsoid to globose, rarely a minority ellipsoid, with somewhat thickened, sometimes compound wall; the outermost layer of the wall smooth, amyloid; hymenophoral trama regular to subirregular; subhymenium subcellular; basidia normal but sometimes 2 spored; cystidia present or absent (sometimes only cheilocystidia present, in other cases hardly any cystidioid bodies present) but often inconspicuous; stipe moderately thick, usually central, solid or becoming tubulose, not insititious; context consisting of usually nonamyloid (but in some species some hyphae weakly amyloid) tissue; all hyphae with clamp connections, never incrusted by bright colored pigment. On decayed trunks, logs, fallen branches, charcoal, and on the soil or leafmold.

Development of the carpophores: Unknown.

Area: Temperate zone and subtropical zone.

Limits: This genus has been emended three times by the inclusion of species of *Omphalia* (Fr.) Quél. sensu lato and *Collybia*. The first emendation (Singer, *l. c.*) concerned species with smooth spores and cystidia (subgen. *Myxomphalia*); in spite of Josserand's disagreement, the author has maintained this emendation in later papers and is still fully convinced that the species in question are congeneric with

the species (or group of species) with triple-walled spores (see *Ann. Myc.* 41 : 61-62. 1943). The resulting genus is considered as natural.

The second emendation was proposed by Singer (apud Vasilieva, *Utch. Zap. Kazansk. Univ.* 99 : 50. 1939) which involved the inclusion in *Fayodia* of *Collybia lacerata* (subgenus *Clitocybula*), i. e. of species with non decurrent lamellae and scattered inconspicuous cystidia (mostly near the edge, and rather inconstant). This emendation should also have included *Collybia familia*, an American species which was then transferred to *Baeospora* because of the lack of data on similar species, all of them American, which would have shown the connection between *F. familia* and *F. lacerata*. Only the type studies on American species started by the author in 1941 revealed this fact. The resulting third emendation, i. e. the inclusion of *F. familia*, a species with frequently subfree lamellae and almost mycenoid habit, was proposed in *Lloydia* 5 : 127. 1942.

All these changes, clearly expressed in the present diagnosis, are not in need of additional explanations. The elements entering the genus are all — though more closely allied to each other than to any other group of agarics — somewhat isolated by strong hiatus, and in order to express this situation adequately, the author (1943) has proposed subgeneric rank for each of the various components.

State of knowledge : Ten species have been studied carefully by modern authors.

Practical importance : *F. maura* contains an antibiotic substance.

SPECIES

Subgenus I. **Eu-Fayodia** Sing. (1943). Cheilocystidia distinct ; no other cystidia present ; main spore wall distinctly compound, triple, the episporium uneven ; lamellae decurrent.

F. bisphaerigera (Lange) Kühn. (Omphalia, Lange ; Omphalia striaepilea sensu Ricken).

Note : The 2 spored form is typical, and by far more common than the 4-spored form. It is quite possible that at least two species are hidden in this section.

Subgenus II. **Myxomphalia** (Kühn. ut sect. *Mycenae*, Sing. (1943). Pleurocystidia often present ; cheilocystidia distinct and numerous ; spores with a somewhat thickened wall but seemingly simple and smooth or subsmooth ; lamellae decurrent.

Type species : *F. maura* (Fr.) Sing.

F. maura (Fr.) Sing. (Omphalia, Quel.); *F. invita* (Karst.) Sing. (Omphalia, Karst.).

Subgenus III. **Clitocybula** Sing. (1943). Cystidia inconstant on the sides and even on the edges of the lamellae; sometimes a few scattered inconspicuos cheilocystidia present; spores as in subgen. II; lamellae subfree to adnate, or adnate to decurrent, in the same specimen. On decaying wood.

Type species: F. lacerata (Lasch) Sing.

F. lacerata (Scop. ex Lasch) Sing. (Collybia, Gillet; Collybia platyphylla var. lacerata Konr. & Maubl.); *F. aperta* (Peck) Sing. (Clitocybe, Sacc.); *F. abundans* (Peck) Sing. (Collybia, Sacc.); *F. oculus* (Peck) Sing. (Omphalia, Sacc.); *F. familia* (Peck) Sing. (Collybia, Sacc.; Baeospora, Sing.); *F. atrialba* (Murr.) Sing.; (Clitocybe, Murr.); *F. tilieti* Sing.

KEY TO THE SPECIES

Considering the small number of species and the completeness of the descriptions available, a key is unnecessary at this instance.

64. HYDROPUS (Kuhn.) Sing.

Lloydia **5**: 129. 1942, nom subnud.; *Pap. Mich. Acad. Sc. Arts & Lett.* **32**: 127. 1946 (publ. 1948).

Type species: H. fuliginarius (Batsch ex Fr.) Sing.

Syn.: Mycena subgen. *Eu-Mycena*, group *Spuriae* 3° (section ?) *Hydropus* Kühner *Le Genre Mycena*, p. 531. 1938, nom. nud.

Characters: Habit between mycenoid collybioid and omphalioid, more often near the latter; pigment, if present in dusky, dull colors, or black; pileus with an epicutis of fascicles or tufts of cheilocystidia-like dermatocystidia, or the latter forming a continuous layer, or fragments of one (becoming fragmentary in age); the dermatocystidia broad to very broad, often filled with fuscous cell sap, rounded above; lamellae adnexed or more or less adnate to subdecurrent or decurrent; spore print white; spores hyaline, smooth, ellipsoid or short-ellipsoid, amyloid (but usually not as strongly amyloid as in *Fayodia*); cheilocystidia versiform, usually rather broad and rounded above; basidia normal; trama nonamyloid; all hyphae with clamp connections; conducting elements sometimes numerous, dark or

« metallic » and context blackening and succulent. On wood, humus, etc.

Development of the carpophores: Unknown.

Area: Cosmopolitan,

Limits: This genus is easy to delimit from all other genera. It is closest to *Mycena* from which it differs in the broad cuticular elements, and the nonamyloid trama (but see under *Mycena*, p. 352).

State of knowledge: After the completion of several series of type studies it is now possible to state that there are at least eight species of *Hydropus*, all completely described as for anatomical, chemical, and macroscopical characters.

Practical importance Probably none.

SPECIES

H. marginellus (Pers. ex Fr.) Sing. (Mycena, Quél.; Omphalina, Quél); ***H. frater-niger*** Sing.; ***H. fuliginarius*** (Batsch ex Weinm.) Sing. (Collybia, Gillet; Agaricus nigritus, Berk. & Curt.; Collybia, Sacc.; Agaricus atramentosus Kalchbr.; Collybia, Sacc.; Mycena, Hoehn.; Agaricus succosus Peck; Collybia, Sacc.; Collybia nigrescens Quél.); ***H. africanus*** Sing.; ***H. atriceps*** (Murr.) Sing. (Gymnopus, Murr.); ***H. translucens*** (Murr.) Sing. (Camarophyllus, Murr.); ***H. Sabalis*** Sing.; ***H. oculatus*** (Murr.) Sing. (Clitocybe, Murr.); obviously also *H. Taxodii* (Murr.) Sing. (Mycena, Murr.); ***H. umbrinus*** (A. H. Smith) Sing. (Mycena, A. H. Smith); ***H. arenarius*** (A. H. Smith) Sing. (Mycena, A. H. Smith), and probably many more.

KEY TO THE SPECIES

The species indicated above can easily be determined by comparing the original and emended descriptions; a key appears to be unnecessary

65. **MYCENA** (Pers ex Fr.) S. F. Gray

Nat. Arr. Brit. Pl. 1: 619. 1821.

Type species: Mycena galericulata (Scop. ex Fr.) Quél.

Syn.: *Gymnopus* (Pers ex) S. F Gray, *Nat. Arr. Brit Pl.* 1: 604. 1821.
Mycenula Karst., *Medd Soc. Faun. Fl. Fenn.* 16: 89. 1889.
Prunulus Caes ex S F Gray sensu Earle (Murr, non Sing. & Sm) *Bull. N Y. Bot. Gard.* 5: 427. 1909.
Insiticia Earle, *l. c.* p. 425.

Basidopus Earle, *l. c.* p. 426
Collopus Earle, *l. c.*
Galactopus Earle, *l. c.*
Stereopodium Earle, *l. c.*
Linopodium Earle, *l. c.*
Pseudomycena Cejp, *Publ. Fac. Sc. Univ. Charles*, p. 138. 1930.
Phlebomycena Heim, *Revue de Mycol.* 10 : 26. 1945 (haud legitime editum nomen).
? *Eomycenella* Atk., *Bot. Gaz.* 34 : 37. 1902.
? *Leiopoda* Vel., *Novit. Mycol. Noviss., Op. Bot. Cech.* 4 : 35. 1947.
? *Retocybe* Vel., *l. c.*, p. 33.

Characters : Habit of the carpophores mycenoid or omphalioid (in the latter case epicutis of the pileus never consisting of smooth filamentous hyphae); pigment present, or absent, bright colored, or dull colored; pileus usually thin and pellucid, striate; epicutis of the pileus usually consisting of diverticulate (Pl. XVI, 1), filamentous or elongate and irregular hyphae, much more rarely these diverticulate hyphae hair-shaped (Pl. XIV, 1), or they are filamentous but smooth, or they are globose and smooth (*M. rorida*-group); if the epicuticular hyphae are smooth the spores are distinctly amyloid; hypodermium and subcutis more or less individualized, one of the layers underneath the epicutis often gelatinized (then the pileus viscid), or consisting of large, short elements (subcellular); hymenophore usually distinctly lamellate; lamellae ascendant, horizontal or descendant, subfree to decurrent; hymenophoral trama subregular to regular or almost subcellular (consisting of rather large and short elements), usually strongly amyloid, rarely very slightly amyloid and the spores also very slightly amyloid (but then base of stipe — a pedestal, or else both pileus and stipe viscid to glutinous); spores usually forming a pure white, more rarely pale cremeous print, hyaline, smooth, with homogeneous, thin, amyloid (rarely nonamyloid — but then pileus and stipe glutinous, or at least the pileus distinctly viscid, or base of the stipe — a pedestal, or else epicutis typically diverticulate) wall; basidia normal but often 1-3-spored as well as 4-spored; cheilocystidia present, other cystidia also often present; stipe central, sometimes with latex (with numerous laticiferous hyphae), usually very thin, fragile to subcartilaginous, insititious or not, usually tubulose; veil none; context fleshy, not reviving; tissue of the stipe usually amyloid; hyphae with numerous clamp connections, at least in the « normal », i. e. heterothallic, 4-spored races. Carpophores attached to the substratum (bark, living

or decaying wood, *Pteridophyta,* moss, dead needles or foliage, charcoal, cones, sticks, humus and sand, or other kinds of soil) by a disc (pedestal), directly, or with a pseudorhiza; mycelium hardly forming mycorrhiza, without connection with black rhizomorphs, often luminescent.

Development of the carpophores: Gymnocarpous. Kavina claimed to have observed what amounts to hemiangiocarpous development in several species of *Mycena,* but Kühner repudiated this indication on the grounds tha Kavina had not seen sufficiently young stages. It is not quite obvious that this discrepancy is entirely due to faulty observation. With so few species studied ontogenetically, one may, theoretically at least, admit the possiblity that there are two groups of *Mycenae*, one gymnocarpous, another hemiangiocarpous. On the other hand, in view of the close relationship between all the species of *Mycena,* this appears rather improbable, and the fact that all species studied by Kühner were gymnocarpous, and all studied by Kavina were hemiangiocarpous can also more easily be interpreted by differences in the manner of observation. The author is inclined to think, therefore, that an error must have ocurred in the observations of either one of the authors cited above, and it is easier to believe that the error has occurred to Kavina because of the ample descriptive and illustrative material published by Kühner, — material that appears to be conclusive enough.

Area: Cosmopolitan, but there are more species in the temperate zone than in the tropics (at least in America).

Limits: The limits of *Mycena* are not final, as outlined in this scheme. Kühner, in his monograph, has strongly emphasized the amyloid reaction of the spores and the tissue, admitting at the same time, several exceptions, such as *Mycena pseudopura* which the author has subsequently transferred to the genus *Poromycena,* also several species in other groups which are, however, so abundantly characterized as *Mycenae* that the absence or slowness of the iodine reaction in either the spores or the tissue does not contest the validity of Kühner's classification, or its practical usefulness. On the other hand, A. H. Smith in an equally valuable and interesting treatment of the genus, has intentionally underemphasized the iodine reactions, obviously for practical reasons of presentation and determination. Kühner's and Smith's classifications are not irreconcilable. However, in Smith's treatment, one is occasionally puzzled when attempting to establish the final position, in a Kühnerian scheme, of a

species described by Smith between 1937 and 1947 (thus not represented in Kühner's monograph) and inserted in one of Smith's mixed groups. It is not the place here to discuss whether or not the chemical classification or the morphological classification are preferable. However, these few species which do not fit in Kühner's scheme affect the delimitation of the genus *Mycena,* and should be discussed here. The author has not had occasion to study all the species concerned. Some of the remarkable species, according to their description, are *M. pusillissima, M. litoralis, M. monticola.* Only the type of the latter has been examined by the author. It appears that this is a true *Mycena* with weak amyloid reaction. The spores are definitely not all amyloid, nor are any of them distinctly amyloid when the usual procedure is followed (hydrolysis with ammonia, then addition of Melzer's reagent). The tissue becomes very slowly and slightly amyloid when the usual procedure is followed. But if the hydrolysis is effected with concentrated hydrochloric acid, the reaction becomes strong and beautifully vinaceous. This species would always remain in *Mycena* rather than in *Poromycena,* even if the amyloidity of the spores were nil because of the characters of the epicutis which consists of thin, flexuous, interwoven hyphae which are strongly nodose and emitting secondary branchlets at oblique as well as at right angles. Though this structure is neither typically diverticulate nor typically astrostromelloid, it is characteristic enough for species with the *Mycena* type of cortical layers, and should not be confused with the structure in *Poromycena.* Aside from that the lamellae are ascendant in the young specimens Another case is *Omphalia lilacifolia,* a species which has been transferred to *Clitocybe* by Singer (1942), and to *Mycena* by Smith (1947). It is obvious that this species does not belong in *Omphalia* but it has nonamyloid spores and nonamyloid tissue, and it cannot be considered as belonging in *Mycena* unless the genus *Mycena* is emended so as to accommodate species without any positive iodine reaction If one studies carefully the taxonomy of the small Clitocybes and that of the glutinous and viscid *Mycenae,* one is led to prefer Smith' solution. This does not mean that the iodine reaction is not good for the generic delimitation of *Mycena,* but the diagnosis must be worded so as to admit certain species with nonamyloid walls. This will not affect the delimitation of the genus *Marasmiellus* (= *Hemimycena*) which, essentially, is closer to *Marasmius* than to *Mycena,* but undoubtedly intermediate between the two.

If the iodine reaction is handled with care and as a character often useful in the generic and specific taxonomy of *Mycena* and related genera rather than schematically or with the intention to lead it ad absurdum (which can of course be done by exaggerating the importance of the exceptions), one will find that it supplements rather than it fixes the generic description of *Mycena*.

The author can fully understand Kühner's and Smith's reluctance to divide the genus *Mycena* in smaller units and recognize it as a small emended unit. Their subject is *Mycena* in the Friesian sense, and treating this large group, they noticed that some of the species described by Fries in tribes other than *Mycena*, could scarcely be separated from *Mycena*. However, when endeavoring to reclassify the group of genera here involved according to modern methods of classification, one cannot but wonder whether a genus of this monstrous size and containing so many clear cut sections as *Mycena* in the sense of Kühner or Smith is still a genus on the same level as the smaller natural genera in the agarics such as *Leucopaxillus* or *Melanoleuca*, or even the large natural genera such as *Russula*. The author is convinced that, both for practical and for theoretical reasons, *Mycena* should be understood in the narrower sense. Everyone realizes that, in order to do so, an unreasonably large number of species, even such species that would otherwise be well known and easily recognizable, must go into the list of species incompletely known, and this interferes with the arrangement of a monographic study. However, such difficulties do not restrain the arrangement of the present work, and consequently, certain species which are not yet quite clearly understood and not fully studied in every regard considered as important in the present arrangement, are left out of consideration until further study will determine their place in the classification.

State of knowledge: Notwithstanding the difficulties encountered in certain forms, especially such with reportedly irregular or unusual iodine reaction, the general knowledge of the species of *Mycena*, is much better than the somewhat confused nomenclatorial situation may suggest. In this regard, the ratio between the state of knowledge on one hand and the disagreement about some names on the other are comparable in *Mycena* and *Russula*. In both genera two monographs have been published, both based on modern research methods, but the older names are often interpreted in different ways.

It appears to the author that in the matter of European species

any non European region, is not important. While some of Smith's reasons for different interpretations seem, at least to the non-specialist, quite convincing, they often are difficult to accept because of European traditions, and European phytogeographic considerations. Besides, it ist almost certain that Kühner's monograph is taxonomically accepted in most European herbaria and laboratories as Smith's is in America, and the author would have continued (as he did in 1943) to use Kühner's nomenclature in spite of his personal preferences in certain cases, were it not for the fact that Smith has not followed such a policy regarding the European species. Under these circumstances, it seems to be correct to adopt a certain definite policy as to the acceptance or non acceptance of names in *Mycena*, or else two nomenclatorial schools will perpetuate themselves. The author believes that if tradition and text of the Friesian diagnosis is not clearly and undubitably on the side of one author, then, in case of disagreement, the names involved should be considered as « nomina dubia ». Without regard as to whether or not future taxonomists will have a list of nomina dubia in *Mycena* (and other genera with a similar nomenclatorial situation) at their disposal, these names are here disregarded, and newer binomials are substituted. If a European species is interpreted by only one author without disagreement on the side of any other modern author, this interpretation is here accepted, but the words « sensu X » are added to the binomial. This is done even in the case of lectotypical material from America, but in the latter case the author is rather pessimistic about the final outcome. Such « tele interpretations » take it for granted that there is no difference in the mycological flora of Europe and the temperate zone of North America, and that all species occurring in this country must also occur on the other side of the Atlantic. This is of course not so; and consequently, misdeterminations may result which are more troublesome than the possible synonyms which might occasionally result if such species were described as new.

Aside from these difficulties, the number of species completely known and ready to be inserted in any classification of the genus *Mycena*, is comparatively large. This is due to the fact that two unusually industrious and ingenious monographers have studied the Mycenas of both Europe and North America, and some few species were added from Northern Asia and the Caucasus. Nevertheless, the species of *Mycena* from Africa, Southern and Eastern Asia, Australia, and Oceania, and those from South and Central America have

scarcely been touched. It is desiderable that now, after so much valuable work has been done in Europe and North America, a world monograph be written representing the actual knowledge on the *Mycenae*

Below, the species known have been sifted twice. In the first place, only those known in every aspect are admitted, and in the second place, only those that do not cause any doubt as to their position have been chosen to illustrate the sections, subsections, and stirpes. This policy has reduced the species to 153, a figure which will from now on steadily grow in accordance with further type studies mainly on species from regions where the *Mycena* flora has thus far not been sufficiently studied.

Practical importance: It is probable that Mycenas, even in the narrower sense, cause various plant diseases in the tropics but few details are available at present. The only definite knowledge we have, concerns *M. flavida* which is pathogenic on *Coffea* (American Coffee Leaf Disease, or Ojo de Gallo). Certain species have been indicated as edible or poisonous but none is of any economic importance. True mycorrhizal relationship between forest trees and Mycenas is improbable but endotrophic mycorrhiza may be formed by some exotic species.

In view of the comparative easiness of growing Mycenas in the laboratory, it is not surprising to see that many data on sexuality of the *Agaricales* are based on material that belongs in this genus.

SPECIES [53]

Sect. I. **SACCHARIFERAE** Kühner (1938). « Species without... [54] basal disc or with a very narrow one; covering of the pileus by no means gelatinized, including a large number of inflated-vesiculose

[53] The classification used here is based on that published in 1943 (*Ann. Mycol.* **41**: 137. 1943) which is in turn based on Kühner's most recent classification (1937 [1938]). However, in the light of Smith's new monograph and certain modifications in line with the author's own investigations it became desirable to change the classification in a few details. The most striking differences between this and the 1943 classification are the abandonment of the subgenera, and the emphasis on some formerly less conspicuous but, as it seems, important and well defined groups as the section *Purae* (= *Janthinae*) and the *Viscidipedes* in a wider sense, as used by A. H. Smith.

[54] Kühner includes here the character « without blue-green colors ». This, however, may not always be true since forms of *M. Mucor* and *M. tenerrima* can

cells... ...which are densely diverticulate and broom like » (dendrophysoid).

Type species : M. tenerrima (Berk.) Sacc.

M. tenerrima (Berk.) Sacc. sensu Lange, Kühner ; *M. osmundicola* Lange.

Sect. 2. **BASIPEDES** (Fr. ut sect. *Agarici* trib. *Mycenae*) Kühner em. Kühner (1926), « Species without blue green colors, stipe at the base abruptly broadened into a disc which is formed by short, inflated, fusiform or ellipsoid hyphae ; covering of the pileus distinctly gelatinous ». Kühner.

Type species : M. stylobates (Pers. ex Fr.) Quél.

M. stylobates (Pers. ex Fr.) Quél. sensu Schroeter ; *M. Mucor* (Batsch ex Fr.) Gillet sensu Lange ; *M. Gaultheri* A. H. Smith ; *M. clavularis* (Fr.) Gillet sensu Kühner ; *M. bulbosa* (Cejp) Kühner ; *M. longiseta* Hoehnel.

Sect. 3. **VISCIPELLES** Kühner (1931) (*Cyanescentes* Kühner 1938). « Stipe not broadened into a disc at the base which is often colored blue or green, entirely pubescent under a lens; covering of the pileus gelatinous. » Kühner.

Type species : M. cyanorhiza Quél. sensu Kühner.

Note : Sect. *Insiticiae* Kühner non Fr. is the same as *Cyanescentes* Kühner. It is based on *M. pachyderma* Kühner which Smith thinks is transitional to the *Corticolae*, i. e. to stirps *Corticola* in our present arrangement. One may be tempted to replace the *Insiticiae* Kühner by a legal sectional name and separate them from the *Cyanescentes* and the *Typicae*, including *M. pachyderma* and *M. chlorinosma*, but this matter must be left to the student specialized in the group.

M. cyanipes Godey (nom. nov.) (M. cyanescens Vel. non Mont.); *M. amicta* (Fr.) Quél. sensu Hoehnel (Prunulus caesiialbus Murr.) ; *M. cyanorhiza* Quél. sensu Kühner ; *M. pachyderma* Kühner ; *M. chlorinosma* Sing. ; *M. flavida* (Maublanc & Rangel) Sing. (Omphalia, Maublanc & Rangel) would seem to belong here but may rather be assigned to a new section.

Sect. 4. **RIGIDIPEDES** Fr. ut sect. *Agarici* trib. *Mycenae* (1836). Pileus and stipe confluent, i. e. not separated by a separation layer as in the first three sections ; stipe neither containing a latex nor covered with a glutinous sheath ; pileus without a gelatinous pellicle ; pigment dull colored, or else with an epicutis consisting of diverticulate hyphae (or hyphae at least nodose ramose).

Type species : M. galericulata (Scop. ex Fr.) Quél.

Note : The sections *Calodontes* Fr. (1836), *Alcalinae* Konr. & Maubl. (1924-37), *Polygrammae* Konr. & Maubl. (1924-37), *Galericulatae* Konr. & Maubl. (1924-37), and *Typicae* Kühner (1938), also most of the *Fragilipedes*, *Filopedes* and *Insiticiae* Fr. are identical, and so is the subgenus *Pseudomycena* Cejp. Unless these names will be used, in the future, for the designation of sections to be split from the sections *Rigidipedes*, or for the designation of subgenera, they must be considered as synonyms of the *Rigidipedes*.

Subsect. **Granulatae** (Lange, p. p.). Cheilocystidia of Lange's type II, or dendrophysoid, i. e. usually vesiculose to clavate, rarely of some other shape, with short to long cylindric appendages over the upper portion, or over most of their surface which gives them an echinate appearance; rarely only the pleurocystidia warty or echinate on their ventricose sides or on their apices (stirps *Latifolia*).

Type species : M. galericulata (Scop. ex Fr.) Quel.

Stirps **Corticola** (Small species on the cortex of living trees with pruinate stipe and globose to subglobose spores).

M. venustula Quél.; *M. supina* (Fr.) Quél. sensu Lange; *M. pseudocorticola* Kühner; *M. madronicola* A. H. Smith; *M. corticalis* A. H. Smith (non Prunulus corticalis Murr.); *M. corticola* (Pers. ex Fr.) Quél. sensu Pat. (Prunulus corticalis Murr.).

Note : This stirps is well separated from other genera and may be better considered as a subsection within the *Rigidipedes*, or else as an autonomous section between the *Cyanescentes* and *Rigidipedes*. If so, the name *Supinae* used by Konrad & Maublanc should not be discarded in favor of the Friesian name *Insiticiae* since the latter has been emended so as to designate the group called « stirps *Polyadelpha* » here.

Stirps **Polyadelpha** (Very small species without basal rhizoids or with long mycelial filaments which radiate from the insititious base; edge of the lamellae not differently colored).

M. capillaris (Schum. ex Fr.) Quél. sensu Lange; *M. Smithiana* Kühner; *M. tubarioides* (R. Maire) Kühner; *M. Lohwagii* Sing.; *M. herbarum* Sing.; *M. juncicola* (Fr.) Gillet sensu Smith; *M. Quercus-Ilicis* Kühner; *M. polyadelpha* (Lasch) Kühner (Omphalia, Quél.; Delicatula, Cejp; Marasmius, Pat.); *M. pterigena* (Fr.) Quél.

Stirps **Elegans** (Edge of lamellae discolored because of a dissolved pigment inside the cheilocystidia, or else pileus bright colored but then epicutis consisting of distinctly diverticulate hyphae and spores strongly amyloid).

M. aurantiomarginata (Fr.) Quél. sensu Schroeter [M. elegans (Pers. ex Fr.) Quél. sensu Kühner]; *M. chlorantha* (Fr. ex Fr.) Gillet sensu Oort [M. elegans (Pers. ex Fr.) Quél. sensu Smith]; *M. flavescens* Vel.; *M. luteolorufescens* Karst; *M. strobilinoides* Peck; probably also *M. Beardsleeana* Sing.

Stirps **Rosella** (Edge darker colored than the sides of the lamellae; the latter with smooth fusoid ampullaceous cystidia).

M. rosella (Fr.) Quél. sensu Schroeter, and (if identical) sensu A. H. Smith.

Stirps **Monticola** (Pileus brightly colored; spores extremely weakly amyloid; epicutis consisting of nodose and somewhat ramose filamentous hyphae; lamellae with concolorous edge).

M. monticola A. H. Smith; perhaps also *M. subincarnata* (Peck) Sacc.

Stirps **Galericulata** [93] (Pileus usually not bright colored, or if bright colored, not combining the characters of either stirps *elegans* or stirps *monticola*).

M. piceicola A. H. Smith; *M. plicosa* (Fr.) Gillet sensu Smith; *M. subplicosa* Karst. sensu Smith; *M. Kuehneri* Sing.; *M. iodiolens* Lundell [M. vitilis (Fr.) Quél. sensu Kühner vix Fr.]; *M. urania* (Fr.) Quél. sensu Smith; *M. psammicola* (Berk. & Br.) Sacc. sensu Smith (an Berk. & Broome ?[94]); *M. Peyerimhoffii* R. Maire; *M. xantholeuca* Kühner; *M. pusilla* A. H. Smith; *M. alcaliniformis* (Murr.) Murr.; *M. atroalboides* (Peck) Sacc.; *M. galericulata* (Scop. ex Fr.) Quél. sensu auct. plur. e. gr. Schroeter (M. Atkinsonii House; M. atrofusca Murr.); *M. hemisphaerica* Peck; *M. rugulosiceps* (Kauffm.) Kühner; *M. permixta* (Britz.) Sacc. [M. megaspora Kauffm.; M. excisa (Lasch) Gillet sensu Bres. non al.]; *M. occidentalis* (Murr.) Murr.; *M. maculata* Karst. [M. alcalina (Fr.) Quél. sensu Ricken; M. parabolica (Fr.) Quél. sensu Bres.; M. rugosoides Peck]; *M. tintinnabulum* (Fr.) Quél. sensu Schroeter; *M. inclinata* (Fr.) Quél. sensu Kühner; *M. pseudoinclinata* A. H. Smith; *M. alnicola* A. H. Smith; *M. paraboliciformis* Sing. (nom.

[93] Formerly (1943), the author distinguished the stirps *Galericulata* from another stirps, *Vitilis*, the latter corresponding to Kühner's group *Filipedes* (an emendation of Fries' *Filipedes* but without distinct rank, subordinated to a subsection. It seems that it is impossible to draw a clear line between the two groups.

[94] Unless this species, in the sense of Smith, is proved to occur in Europe, the application of the name *M. psammicola* to the American species is at least debatable.

nov.) [M. parabolica (Fr.) Quél. sensu Smith]; *M. radicatella* (Peck.) Sacc. (Prunulus adirondackensis Murr.; M. subviscida, Kauffm. & Smith); *M. longipes* (Murr.) Murr. (Prunulus magnus Murr.).

Stirps **Cinerella** (Differs from the preceding stirps in having a very distinct omphalioid habit, horizontal, arcuate-decurrent lamellae, and relatively less thin stipe; pigment always dull colored (gray or fuscous); if the epicutis consists of inflated erect bodies forming a palisade or isolated fascicles — see under sect. *Viscidipedes*, subsect. *Roridae*, note, p. 362).

M. cinerella Karst. sensu Lange; *M. subconcolor* A. H. Smith; *M. concolor* (Lange) Kühner.

Stirps **Latifolia** (Differs from the preceding stirpes in having pleurocystidia which are projecting and fusoid like those of the *Ciliatae* but dendrophysoid-echinate either in the middle portion or at the apex; habit omphalioid).

M. latifolia (Peck) Sacc. (M. pinetorum Lange).

Stirps **Borealis** (Differs from the preceding stirps in having mycenoid instead of omphalioid habit).

M. borealis A. H. Smith; *M. Font Queri* R. Maire.

Subsection Ciliatae (Lange p. p. 1914) Kühner (1938). Pleurocystidia either absent or not echinate but smooth; cheilocystidia always smooth and simple to branched, not clavate and echinate.

Type species: M. alcalina (Fr.) Quél. sensu Schroeter.

Stirps **Quisquiliaris** (with the same characters as stirps *Cinerella*, but with the cystidia of the type I of Lange, i. e. not the type described under the subsection *Granulatae*).

M. quisquiliaris (Joss.) Kühner; *M. Brownii* A. H. Smith; *M. pseudoclavicularis* A. H. Smith.

Stirps **Rubromarginata** (with the same characters as stirps *elegans*, but with the cystidia of the type described under subsection *Ciliatae*,.

M. capillaripes Peck (M. Langei R. Maire); *M. debilis* (Fr.) Quél. sensu Smith and Fries; *M. citrinomarginata* Gillet; *M. cedretorum* R. Maire; *M. arenacea* (Fr.?) Quél. sensu Schroeter, Kühner, A. H. Smith; *M. albidolilacea* Kühner & Maire; *M. viridimarginata* Karst.; *M. olivaceoalcalina* Sing.; *M. atromarginata* (Lasch) Gillet; *M. rubromarginata* (Fr.) Gillet; *M. elegantula* Peck; *M. purpureofusca* Peck; *M. luteoalcalina* Sing.; *M. flavipes* Quél. (M. Renati Quél.); *M. Seynii* Quél.; *M. rhaeborhiza* (Lasch) Gillet (M. lutea Bres.); *M. chrysoco-*

Stirps **Alcalina** (with characters of stirps *Galericulata*, but with the cystidia of the type described under subsection *Ciliatae.*)

M. zephirus (Fr.) Quél.; *M. strobilicola* Favre & Kühner (M. vernalis Post ex Landell non Vel.); *M. alcalina* (Fr.) Quél. sensu Schroeter, Kühner, A. H. Smith; *M. chlorinella* (Lange) Sing. [M. alcalina var. chlorinella Lange; M. metata (Fr.) Quél. sensu Schroeter; M. leptocephala (Pers. ex Fr.) Gillet sensu Ricken]; *M. macrocystidiata* Sing.; *M. atrocyanea* (Batsch ex Fr.) Gillet sensu Kühner (M. nigricans Bres.); *M. fragillima* A. H. Smith (M. Vasilievae Sing.); *M. actites* (Fr.) Quél. sensu Ricken; *M. plumbea* (Fr.) Karst. sensu Smith, an Fr.; *M. subvitrea* A. H. Smith; *M. griseoconica* Kauffm.; *M. praecox* Vel.; *M. niveipes* (Murr.) Murr. (M. pseudogalericulata Lange; M. Jacobi Kühner); *M. atroalba* (Bolt. ex Fr.) Gillet sensu Ricken, Singer; *M. tenuiceps* A. H. Smith; *M. Josefi* Sing. (M. atroalba sensu Vel.); *M. algeriensis* R. Maire; *M. excisa* (Lasch) Gillet sensu Smith; *M. sudorella* Sing.; *M. fagetorum* (Fr.) Gillet; *M. pseudovulgaris* Kühner (if different from the subsequent species); *M. laevigata* (Lasch) Quél. sensu Hoehnel, Sing.; *M. polygramma* (Bull. ex Fr.) Quél. sensu Lange; *M. vitilis* (Fr.) Quél. sensu Lange [M. filopes (Bull. ex Fr.) Quél. sensu Schroeter, M. adhaerens Vel.]; *M. pullata* (Berk. & Cooke) Sacc. sensu Smith; *M. Abramsii* (Murr.) Murr.; *M. fuscoovata* A. H. Smith; *M. Kauffmaniana* A. H. Smith; *M. subfusca* A. H. Smith; *M. murina* (Murr.) Murr. [M. stannea (Fr.) Quél. sensu A. H Smith]; *M. pectinata* (Murr.) Murr.; *M. praelonga* (Peck) Sacc.; *M. subsupina* A. H. Smith; *M. rubrotincta* A. H. Smith [M. tenuicula (Murr.) Murr. non (Karst.) Sacc.].

Sect. 5. **LACTIPEDES** Fr. ut sect. gen. *Agarici* trib. *Mycenae* (1836). Stipe with laticifers containing white or colored milky latex (latex not watery); stipe and pileus not viscid.

Type species : M. galopoda (Pers. ex Fr.) Quél.

M. crocata (Schrad. ex Fr.) Quél.; *M. sanguinolenta* (A. & S. ex Fr.) Quél.; *M. subsanguinolenta* A. H. Smith; *M. haematopoda* (Pers. ex Fr.) Quél.; *M. Atkinsoniana* A. H. Smith (M. fagicola A. H. Smith non al.); *M. erubescens* Hoehnel (M. fellea Lange; M. cholea A. H. Smith; M. parabolica sensu Hoehnel; synonymy according to Kühner); *M. galopoda* (Pers. ex Fr.) Quél.

Sect. 6. **GLUTINIPEDES** Fr. ut set. *Agarici* trib. *Mycenae* (1836) *Gummosae* Lange 1914; *Glutinosae* Kühner 1931). Stipe in cross-section showing an outer gelatinous layer; hence usually viscid when fresh, or sometimes covered with a thick glutinous sheath.

Type species : M. epipterygia (Scop. ex Fr.) Quél.

Subsect. **Fuliginellae** A. H. Smith ut sectio (1947). Pileus not with a corticate layer consisting of broad inflated cells (some with brown contents); stipe not yellow or otherwise bright colored. Mycelium humicolous; carpophores not cespitose (but often densely gregarious).

Type species : M. vulgaris (Pers. ex Fr.) Quél.

M. insignis A. H. Smith; *M. clavicularis* (Fr.) Gillet; *M. militaris* Karst.; *M. vulgaris* (Pers. ex Fr.) Quél.; *M. pelliculosa* (Fr.) Quél.; *M. odorifera* (Peck) Sacc.; *M. quinaultensis* Kauffm. apud A. H. Smith; *M. tenax* A. H. Smith.

Subsect. **Gummosae** (Lange) Oort (1928) (sect. *Viscosae* Smith 1947). Pileus without a corticate layer consisting of broad, inflated cells (some with brown contents); stipe yellow or otherwise bright colored. Mycelium humicolous (or on very old decayed wood); carpophores as a rule not cespitose.

Type species : M. viscosa (Secr.) R. Maire.

M. griseoviridis A. H. Smith; *M. viscosa* (Secr.) R. Maire (Agaricus alcalinus viscosus Secr.; M. epipterygia var. viscosa Ricken); *M. epipterygioides* Pearson; *M. epipterygia* (Scop. ex Fr.) S. F. Gray (Prunulus paludicola Murr.); *M. subinamyloidea* Sing.

Subsect. **Caespitosae** A. H. Smith ut sectio (1947). Pileus not with a corticate layer consisting of broad inflated cells (some with brown contents); stipe either orange to yellow, or dull colored to white; mycelium lignicolous; carpophores as a rule fasciculate cespitose, rarely gregarious.

Type species : M. texensis A. H. Smith.

M. glutinosa Beardslee; *M. Austinii* (Peck) Kühner; *M. hondurensis* A. H. Smith; *M. texensis* A. H. Smith; *M. Leaiana* (Berk.) Sacc.; *M. lilacifolia* (Peck) A. H. Smith (Omphalia, Peck; Omphalina, Murr.; Clitocybe, Sing.).

Subsect. **Roridae** Kühner ut sectio (1931). Pileus with a corticate layer consisting of broad inflated cells, some of them with brown contents; stipe neither yellow nor orange; mycelium lignicolous or not; carpophores usually very gregarious but not cespitose nor fasciculate.

Type species : M. rorida (Scop. ex Fr.) Quél.

M. rorida (Scop. ex Fr.) Quél.

Note : This subsection is very isolated among the viscid *Mycenae*, and it appears to be much closer to *Mycena sicanetica* (Sing.) Sing. as

described in *Ann. Mycol.* **41**: 140. 1943 in spite of the fact that the latter has dry stipe. These two species are exactly intermediate between *Mycena* and *Hydropus*, having all the chemical characters of the *Mycenae* and all the anatomical characters of *Hydropus* while the macro-morphological characters are closer to the *Mycenae Viscidipedes* in *M. rorida* and closer to *Hydropus* in *M. seuanctica*. It is at present impossible to tell whether other species will eventually enter this interesting group. The author has inserted it as a subsection in *Mycena* but this is a temporary solution, and it is expected that this group will eventually be separated from *Mycena*.

Sect. 7. **PURAE** Konr. & Maubl (1924-37) (*Ianthinae* Kühner, as A. H. Smith ut subsectio 1947). Pigment rarely dull colored often violet or rose color, etc.; cuticle consisting of a poorly developed subcutis and an equally poorly developed epicutis, the latter consisting of smooth hyphae; both tissue and spores amyloid; carpophores usually rather fleshy with raphanaceous odor, collybioid, clitocyboid, or tricholomatoid rather than mycenoid in some cases.

Type species : M. pura (Pers. ex Fr.) Quél.

Stirps **Pura** (Edge of the lamellae concolorous with the sides).

M. pura (Pers. ex Fr.) Quél.; probably also *M. Kuehneriana* A. H. Smith with small spores and adnato decurrent lamellae, and *M. subaquosa* A. H. Smith which is white. *Phlebomycena madegassensis* Heim obviously belongs here.

Stirps **Pelianthina** (Edge of the lamellae darker colored).

M. pelianthina (Fr.) Quél.; *M. rutilantiformis* (Murr.) Murr. (Prunulus, Murr.; M. pseudopelianthina Lange).

KEY TO THE SPECIES

Kühner (*Le Genre Mycena*, Paris 1938) and A. H. Smith (*North American Species of Mycena*, Ann Arbor 1947) contain excellent keys.

66. POROMYCENA Van Overeem

in Van Overeem & Weese, *Icon. Fung. Malay.* **14-15**: 4. 1926, em. Singer, *Lloydia* **8**: 218-219. 1945.

Type species : P. decipiens Van Ov. in Van Ov. & Weese.

Characters : Habit of the carpophores mycenoid to mycenoid-marasmioid; pigment usually bright (often lilac or greenish); epicutis of the pileus consisting of smooth, hyaline, filamentous hyphae;

dermatocystidia few on the disc, or none; hypodermium subcellular, pigmented; hymenophore lamellate but strongly intervenose often to the point of appearing poroid with the pores arranged radiately, rather broadly adnexed to almost decurrent; spore print white; spores hyaline, smooth, ovoid-oblong to ellipsoid, nonamyloid, with simple wall; cystidia present only on the edge of the lamellae (pores), as cheilocystidia, none on the sides; basidia normal; hymenophoral trama more or less regular; stipe central, with basal tomentum sometimes strongly developed, never insititious, rather thin and fragile to slightly toughish; context consisting of amyloid hyphae; hyphae with or without clamp connections (if there are clamp connections in the epicutis of the pileus, the hymenophore is poroid or almost so; if the hymenophore is lamellate and merely intervenose, the epicutis consists of clampless hyphae), non gelatinized. On humus and débris, sticks and logs, among moss and on anthills.

Development of the carpophores: Unknown, probably gymnocarpous.

Area : Predominantly tropical, but one species temperate.

Limits : The limits against *Mycena* are clearly determined by the chemical reactions in spite of the obvious affinity of the *Pura* group of that genus. In *Poromycena*, the epicutis of the pileus consists of non diverticulate hyphae; the trama is made up of hyphae without clamp connections if the hymenophore is merely intervenose as is often the case in *Mycena* (yet in that genus all normal specimens excepting those that have parthenogenetic development, have clamp connections, as far as is now known); and if there are clamp connections, the hymenophore is so strongly lamellate-anastomosing that it can be termed poroid or almost poroid; the spores are nonamyloid or so slightly amyloid that this reaction can be neglected.

With these characters, *Poromycena* would schematically be inserted near *Marasmius* rather than near *Mycena*. However, the structure of the epicutis, and the affinities with the *Pura*-group of *Mycena* exclude this arrangement; consequently, *Poromycena* has been taken into the subtribus *Myceninae*.

State of knowledge . Five species of this genus have been described recognizably and appear to belong here [17]. Two of them have been

[17] In a recent paper (*Rev. Myc* 10 : 3-60, pl. I-IV. 1945, publ. 1946), R. Heim disposes of two species, *P. myrmecophila* and *P. decipiens* as having nonamyloid trama. These are precisely the two species not studied by the author. The type specimens of these two species should be reexamined as for their iodine re-

studied by the author (1945), but it may be that there are more species not yet recognized as belonging here.

Practical importance : None.

SPECIES

P. pseudopura (Cooke) Sing. (sensu Kühner) (Mycena, Sacc.); *P. viridula* (Berk. ex Cooke) Sing. (Laschia, Cooke); *P. myrmecophila* (Heim) Sing. (Omphalia, Heim); *P. violacella* (Speg.) Sing. (Heliomyces, Speg.; Collybia, Speg.; Poromycena anastomosans Sing.); *P. decipiens* Van Ov. in Van Ov. & Weese.

KEY TO THE SPECIES

A. Clamp connections in epicutis none (Kühner); lamellae slightly intervenose, not poroid. European species. *P. pseudopura*

A. Clamp connections present. Tropical and subtropical species.

B. Lamellae greenish or gray; many or all anastomoses between the lamellae lower than these; species occurring in tropical and subtropical America and on Madagascar.

C. Lamellae greenish; low veins and anastomosing ridges of full lamella-height both occurring in the same carpophore or in associated carpophores; spores 7-7.8 × 4.2-4.8 μ. *P. viridula*

C. Lamellae grayish; all veins lower than the radial lamellae; spores 7.8-10 × 3.5-4.5 μ.

D. Base of the stipe with pale yellow setae; lamellae broad (up to 3-5 mm), arcuate-decurrent and continued at the apex of the stipe; on inhabited anthills on Madagascar. *P. myrmecophila*

D. Base of the stipe not markedly setose; lamellae moderately broad, adnate to subdecurrent; on foliage and palm debris, etc. in hammocks in Florida, and south to Brazil. *P. violacella*

B. Lamellae whitish in the center, more pink toward the margin; most or all anastomoses of equal height with the radial lamellae. Species occurring in tropical Asia. *P. decipiens*

species of *Poromycena* in our sense should be different in their amyloidity. If Heim's indications are confirmed by reexamination of the types under the precautions recommended in the introduction to this work (hydrolization of the wall substance before using the Melzer, and prolonged time of reaction before the final result is observed), it would become necessary to revise the position of such species as have nonamyloid tissue.

67. BAEOSPORA Sing.

Rev. Myc. 3: 193. 1938.

Type species: *B. myosura* (Fr. sensu Quél., Ricken) Sing.

Characters: Habit of the carpophores collybioid; pileus with initially incurved margin, hygrophanous or subhygrophanous; pigment either intracellular or intercellular and incrusting, brown to melleous, or (macroscopically) violet; epicutis and hypodermium well differentiated or little differentiated, the epicutis consisting of more or less radially arranged, filamentous, repent hyphae, but some of the hyphal ends often ascendant or erect, and then occasionally transformed into dermatocystidioid excrescences which, however, are very scattered on the surface of the pileus; hypodermium consisting of somewhat larger hyphae: hymenophore lamellate, lamellae narrow to adnexed to subfree, crowded, pallid or somewhat lilac; hymenophoral trama irregular-subintermixed to regular, consisting of elongated hyphae; basidia small, normal; cystidia present but often very scattered on the sides of the lamellae, and then these appearing on the edges assuming the character of cheilocystidia; spores hyaline, smooth, very small, oblong or cylindric, amyloid, with thin, simple wall; subhymenium forming a thin layer, intermixed-subcellular, consisting of extremely small elements; stipe central with a pseudorhiza or without it, subequal above the substratum, with dermatocystidia (hairs); context pallid to lilac, consisting of nonamyloid hyphae with clamp connections. On wood, on cones of conifers, also on other similar substrata buried in the earth.

Development of the carpophores: Unknown.

Area: Northern temperate zone.

Limits: The genus has initially been conceived somewhat too widely including species with amyloid tissue, or with subglobose spores, such as *Pseudobaeospora oligophylla* and *Fayodia familia*. By excluding these species (Singer 1942), we obtain a very homogeneous, natural small group of species to be retained in *Baeospora*. This genus is then parallel to *Xeromphalina*, obviously the phase of a phylogenetical development where the hymenophore has become nondecurrent, and the spores smaller. There is no difficulty in delimiting the genus *Baeospora* in its present outline.

State of knowledge: The two species entering *Baeospora* are completely known except for the development of the carpophores.

Practical importance: None.

SPECIES

B. myosura (Fr. sensu Quel., Ricken) Sing. (Collybia, Quel.; Mycena, Kühner; Collybia strobilina Velen.; Collybia Friesii Bres.) and its variety var. *Farrei* Sing. [Baeospora myosura spp. varicosa (Fr. sensu Boudier, non Fr.) Favre]; *B. myriadophylla* (Peck) Sing. (Collybia, Peck; Mycena, Kühner; Collybia lilacea Quel.; Collybia teleopanthina Metrod).

KEY TO THE SPECIES

A. Lamellae pallid; on cones (*Pinus, Picea*). Europe ... *B. myosura*
A. Lamellae lilac; on wood (frondose trees). Europe, Siberia, North America. *B. myriadophylla*

68. XEROMPHALINA Kühn. & Maire

Bull. Soc. Myc. Fr. **50**: 18. 1934

Type species: Xeromphalina campanella (Batsch ex Fr.) Kühn. & Maire.

Syn.: Omphalopsis Earle, *Bull. N. Y. Bot. Gard.* **5**: 425. 1909, non Grev. (1863).

Characters: Habit of the carpophores omphalioid or omphalioid-marasmioid; pigment intercellular, incrusting the walls, bright colored; pileus with initially somewhat incurved margin; epicutis consisting of radially arranged, repent, non diverticulate hyphae, without dermatocystidia or palisade; color of the pileus fulvous, vinaceous, etc.; hypodermium, trama (including the hymenophoral trama) with pigment-incrustations which often turn pink to red with alkali; hymenophore lamellate (but sometimes slightly intervenose); lamellae broadly adnate to deeply decurrent, colored; hymenophoral trama regular, its hyphae close, rather voluminous, subparallel and axillarly arranged, with slightly thickened walls; basidia normal; cystidia present on the edge and on the sides of the lamellae, yet in some individuals not very frequent or not very conspicuous, in others very numerous and very conspicuous, hyaline; stipe more or less central, never white, never glutinous, with colored basal tomentum which is always present, often very conspicuous and strigose (ascending along the surface of the stipe while becoming shorter toward the middle of the stipe and reduced from there upward to a yellowish pruina),

never insititious nor arising from a basal disc (pedestal); without veil; context somewhat tough and sometimes reviving; tissue nonamyloid; hyphae with clamp connections; on needles, sticks, stumps and trunks, dead as well as living, on buried wood and on humus,

Development of the carpophores : Unknown.

Area : Temperate zones.

Limits : This genus should be understood in the original sense, i. e. restricted to section *Campanellae* Sing. These are the species with nonamyloid hyphae, with pleurocystidia and colored basal tomentum. This excludes species later introduced by Singer (*Omphalia Typhae* Schweers, *Omphalia Kalchbrenneri* Bres.; *Xeromphalina mesospora* Sing.). The excluded species can be inserted in *Mycena* (if otherwise fitting the generic diagnosis of that genus), or in *Cantharellula* (as in the case of *O. Kalchbrenneri*). The remaining part of *Xeromphalina* is much easier to define than the genus in the wider sense (as tentatively used by Singer in 1942 3), and represents a truly natural unit, closely related to *Heimiomyces*. The latter genus differs in several ways, most distinctly in the structure of the epicutis which includes erect bodies which often form a palisade.

State of knowledge : The species admitted here are all well known in their essential characters. There is still a taxonomic problem to be solved as far as the group of *X. campanella* is concerned. This species always occurs on coniferous wood, but a closely related form occurs on various frondose trees, even living trees, yet, morphologically or chemically, it is at present hardly possible to distinguish it from the typical *X. campanella*.

Practical importance : The fact just mentioned is of some practical importance since *X. campanella* can be used by foresters as a reliable indicator of coniferous wood even in badly decayed condition.

SPECIES

X. campanella (Batsch ex Fr.) Kühner & Maire (Omphalia, Quél.; Omphalopsis, Earle apud Murr.); *X. cauticinalis* (With. ex Fr.) Kühner & Maire (Marasmius, Fr.; Marasmius fulvobulbillosus R. Fries); *X. orickiana* (A. H. Smith) Sing. (Omphalia, A. H. Smith).

KEY TO THE SPECIES

A. Trama not reddening in alkali; lamellae deeply decurrent; circumpolar (On frondose trees, Abies sp., and on coniferous wood) ... *X. campanella*

A. Trama reddening in alkali or lamellae merely adnate-decurrent.

B. Pileus without « dark vinaceous brown » (Ridgway) colors; temperate species. ... *X. cauticinalis*

B. Pileus eventually « dark vinaceous brown »; California ... *X. orickiana*

69. HEIMIOMYCES Sing.

Lloydia **5**: 128, 1942.

Type species: *Agaricus (Collybia) tricolor* Berk. & Curt.

Characters: Habit of the carpophores collybioid to marasmioid; pigment membranal or epimembranal, fulvous to tawny, yellow, etc.; pileus with initially incurved margin; epicutis subhymeniform, consisting of erect elements 1.3-4.5 µ broad, most of them hyaline, few slightly incrusted by the pigment, forming a continuous layer or somewhat scattered outside indefinite areas where they are crowded, a few oblique in *H. fulvipes*; hypodermium strongly pigmented, consisting of large, broad, somewhat irregular but usually elongated hyphae which are more or less thick walled; hymenophore lamellate but the lamellae often intervenose and anastomosing at the ground, yet not enough to make them appear poroid in any known species, adnexed to subdecurrent; often somewhat tough; hymenophoral trama regular to subirregular, consisting of thick walled hyphae; spores small to medium sized, hyaline, cylindric or ellipsoid, smooth, amyloid, with simple thin wall, with slight hilar depression; basidia rather small sometimes with amyloid tip, with rather thin, long, straight sterigmata, without carminophilous granulosity; cystidia numerous at least on the edge of the lamellae, but also often on the sides of the lamellae (where they may be replaced by some kind of pseudoparaphyses which are fusiform, acute, and non projecting); stipe central, velutinous or tomentose, frequently with pseudorrhiza; context consisting of thick-walled, nonamyloid hyphae with clamp connections. On wood.

Development of the carpophores: Unknown.

Area: North, Central and South America; boreal, temperate, subalpine, and subtropical zones.

Limits: This genus differs from *Xeromphalina* in the structure of

the epicutis; from *Baeospora* in larger spores and the larger number of erect hyphae on the pileus; from *Flammulina* in the non-viscid pileus and the amyloid spores; from *Poromycena* in the structure of the epicutis, the amyloid spores and the nonamyloid tissue; from *Filoboletus* in lamellate hymenophore, narrower spores, different covering of the stipe, different pigment, and different attachment to the substratum.

State of knowledge: Two species are known to belong in this genus — both have been studied carefully in all their essential characters, the type species by the author, and the other species by A. H. Smith, who also suggested its congenerity with *H. tenuipes*, and subsequently by the author.

Practical importance: Nothing known.

SPECIES

H. tenuipes (Schw.) Sing. [Collybia, Sacc.; Gymnopus, Murr.; Collybia rheicolor (Berk.) Sacc.; Marasmius rhabarberinus Berk.; Marasmius amabilipes Peck; Collybia aurantella (Speg.) Speg.]; ***H. fulvipes*** (Murr.) Sing. (Gymnopus, Murr.).

70. FILOBOLETUS Henn.

Warburg's *Monsunia* 1: 146. 1900, sensu Hoehnel, em.

Type species: *Filoboletus mycenoides* Henn. sensu Hoehnel.

Syn.: *Laschia*, sect. *Porolaschia* Pat. *Journ. Bot.* 1: 231. 1887, p. p.
Leucoporus, sect. *Gelatinosi* Pat. *Essai tax.* p. 82. 1900.
Leucoporus, sect. *Filipedes* Pat., l. c.
Bactroboletus, Clements, *Gen. Fungi*, p. 108. 1909.
Mycenoporella Van Ov. in Van Ov. & Weese, *Icon. Fung. Malay.* 14-15: 2. 1926.

Characters: Habit marasmioid-omphalioid, or marasmioid-mycenoid, but suggesting a *Polyporus* because of the configuration of the hymenophore; pileus convex; epicutis consisting of thin repent filamentous hyphae which are either smooth or very finely roughened; hypodermium little differentiated but of considerable diameter, denser than the trama of the pileus; hymenophore distinctly poroid, the pores usually not even arranged in a radial manner so as to suggest

the derivation from lamellae, forming a rather deep or a very shallow layer; spore print white, or whitish; spores hyaline, smooth, ellipsoid to short ellipsoid, sometimes ellipsoid oblong or subglobose, amyloid, wall homogeneous; basidia normal; cheilocystidia not always clearly differentiated from the pseudoparaphyses (which often take the shape of epibasidium bearing basidioles, and remain sterile); similar cystidioid bodies or clavate, echinate elements taking the shape of dermatocystidia near the margin or on the disc of some specimens; stipe central, or slightly eccentric, more or less «grafted» to the substratum or truly insititious, without a trace of a pseudorrhiza, subglabrous to pruinose or floccose, not tomentose except sometimes at the base; context consisting of thick-walled hyphae (at least many of them thick walled), very frequently somewhat gelatinized, at least in some portions of the carpophore (not in the stipe), nonamyloid, with clamp connections. On dead wood, more rarely on other dead plant débris (foliage, etc.).

Development of the carpophores : Unknown. cf. fig. 24 in Heim, *Rev. Myc.* **10** : 40. 1945 (1946).

Area : Tropics.

Limits : This genus is sharply separated from other agarics by the truly poroid hymenophore in most forms, and is still well separated from them by the combination of characters, even if the configuration of the hymenophore is not taken into consideration. *Filoboletus* undoubtedly comes closest to *Heimiomyces* (about its delimitation, see under *Heimiomyces*).

There may be some question whether or not Hoehnel's *Filoboletus* is actually, as Hoehnel seems to assume, the genuine species collected for Hennings and described by him. There is a slight divergence in size when both descriptions are compared but not enough — in a group with great variability in size, and in dealing with Henning's inaccurate descriptions — to warrant a distinction between the two specimens on that basis. Hennings' type has undoubtedly been destroyed during the last war, and it appears that the only material that can still be checked upon is that collected by Hoehnel. Consequently, the only reasonable solution now, is to admit *Filoboletus* in the sense of Hoehnel. Otherwise, a clear delimitation of the genus will never be possible, even if some specimens of doubtful identity will be found on Java to fit Hennings' diagnosis.

State of knowledge : Three species out of four to five have been studied thoroughly by the author. One is known, rather well except

for the anatomy of the pore edges and the chemism of the spore wall and tissues; another one may be a variety of *F. gracilis.*

Practical importance : None.

SPECIES

F. mycenoides Henn. sensu Hohnel; *F. manipularis* (Berk.) Sing. (Favolus, Berk. ; Porolaschia, Pat. ; Poromycena, Heim ; Favolus caespitosus Berk. ; Laschia, Berk. & Br. : Polyporus mycenoides Pat.); *F. gracilis* (Klotzsch apud Berk·) Sing. (Polyporus, Klotzsch ; Laschia clypeata Pat. ; Polyporus obolus Ellis & McBride): *F. luteus* (Van Ov. in Van Ov. & Weese) Sing. (Mycenoporella, Van Ov.); probably also *Favolaschia Staudtii* Henn. (but perhaps a variety of *F. gracilis*).

KEY TO THE SPECIES

A. Pileus light pinkish or yellow. Java.
- B. Pileus up to 3 25 mm broad, light pinkish ... *F. mycenoides*
- B. Pileus larger, yellow. ... *F. luteus*

A, Pileus with very little pigment.
- C. Pores 3 6 mm deep. Tropical Asia, Australia, Oceania, Africa ... *F. manipularis*
- C. Pores 0 5-3 mm deep. Tropical America, West Africa ... *F. gracilis*

GENERA INCERTAE SEDIS

Gloiocephala Mass., *Grevillea* 21 : 34. 1892. « Hymenophore circular, plane, the upper sterile surface bearing numerous large projecting cystidia which secrete a considerable quantity of hyaline mucus ; hymenium covering the entire under surface of the hymenophore, and consisting of closely packed basidia, each bearing a single spore at the apex ; stem central, composed of a fascicle of transversely septate hyphae ». Massee. The type species is *G. epiphylla* Mass. The figure, *l. c.*, shows a monostratous layer of isodiametric hyphae forming the epicutis of the pileus from which the large dermatocystidia emerge. The mucus is shown dropping down from the margin. The so-called 1 spored basidia are certainly not basidia but either pseudoparaphyses, or else cystidia with capitate apex. The whole carpophore is whitish. It was collected in Jamaica.

Höhnel thought that this and *Hymenogloea* Pat. are identical.

Without having studied the types of Massee's fungus, it is impossible to judge on the validity of *Gloiocephala*. The strong mucus of the latter genus is certainly remarkable, and the dermatocystidia are also a distinguishing character as far as *Hymenogloea* is concerned. Consequently, all that can be said at present, is that it seems reasonably certain that *Gloiocephala* is close to *Marasmius* and *Hymenogloea*.

Discocyphella Henn. in Warburg's *Monsunia* 1 : 141. 1900. « Pileus thin membranous. subgelatinous, convex or disciform; stipe central, filiform, cartilaginous; hymenium occupyin the lower surface of the carpophores, smooth, glabrous; basidia clavate typically bisporous, hyaline or yellowish ». Hennings. The type species is *D. marasmioides* Henn. Patouillard and Höhnel believed that this genus is merely a somewhat gelatinous representative of the genus *Cymatella* Pat. (see there). This may be so — or not. Since the type specimen has probably been destroyed, there is hardly a way to save this genus from entering the list of the genera dubia.

GENERA IMPERFECTLY KNOWN

Leucoinocybe Sing., *Ann. Mycol.* 41 : 144. 1943, ad interim. « Pileus with an epicutis consisting of non diverticulate elements, with a non-cellular hypodermium, but with free hairs; lamellae subfree, rather broad; spores ellipsoid to almond shaped, amyloid, medium sized; hymenophoral trama regular, nonamyloid; habit of the carpophores of the *Marasmieae* or of *Inocybe* » Singer. The type species is *Mycena lenta* R. Maire. This species has been described in detail by Kühner, *Le Genre Mycena*, p. 530 under « *Xeromycena* » which is Kühner's equivalent for the genus *Baeospora*. However, *M. lenta* differs in several important characters from *Baeospora*. Since *Leucoinocybe* is thus far monotypic, and its affinites not quite clear, the author hesitates to insert *Leucoinocybe* in the series of numbered genera of the *Mycenineae*, thereby conserving its interim status.

Eomycenella Atk., *Bot. Gaz.* 34 : 37. 1902. « Plants stipitate; pileus campanulate to expanded consisting of a layer of radiating threads forming a more or less lattice-like or trabecular, expanded, thin structure; trama wanting or very rudimentary, the subhymenium arising directly from the trabeculae of the pileus; hymenium plane, or in larger forms with a few short, narrow, distant lamellae, not reaching the stipe; lamellae with rudimentary trama; basidia

clavate, 4 spored; spores smooth, 1 celled, hyaline; stipe fleshy, deli cate; at maturity hymenium dissolving, leaving many of the spores lying on an amorphous layer against the trabeculae. One species, on decaying leaves of *Rhododendron maximum*, Blowing Rock, N. C.». The type species is *E. echinocephala* Atk. (with figure 1, *l. c.*). The de scription of this species suggests a close relationship with the *Osmun dicola* group of *Mycena*. This cannot be proved at present since type studies are impossible. But whatever the iodine reactions of the original material would have been, it is very unlikely that *Eomycenella* is a valid genus, even if good material from the type locality should become available on the same host. The somewhat reduced lamellae alone are by no means a generic character in this group unless ac companied by other more important characters. A. H. Smith also tends to consider *Eomycenella* as a synonym of *Mycena*, yet, in the broader sense of Kühner.

Tribus BIANNULARIEAE Sing.

Ann. Mycol. **34**: 330. 347. 1936

Type genus. *Biannularia* G. Beck (= *Catathelasma* Lovej.).

Syn.: Armillarieae Imai, *Journ. Fac. Agr. Hokkaido Imp. Univ* **43**: 46. 1938 (spec. & diagn. exclusis

Characters: Lamellae decurrent or adnate to sinuate adnexed, inserted or with very few lamellulae; hymenophoral trama bilateral in young specimens, nonamyloid: spores oblong and large, smooth, hyaline, or short ellipsoid to ellipsoid and medium sized, always amyloid, smooth, with thin wall; stipe fleshy; veil present, more or less distinctly double in most species, but no basal volva present.

Note: This tribus is rather isolated among the white spored agarics. Its position is between the tribus *Leucopaxilleae* of the *Tricholo mataceae* and the family *Amanitaceae*. It differs from all *Tricholo mataceae* in the bilateral trama, and from the *Amanitaceae* in the adnexed to decurrent lamellae. Unfortunately, it is impossible to express, in a linear arrangement, the intermediate position in a better way than has been attempted here. The *Leucopaxilleae* are, at the same time, too close to the *Clitocybeae* to be separated from them by the group of pleurotoid and marasmioid mycenoid tribus. Aside from

from the *Hygrophoraceae*, or from some ancestor intermediate between the *Biannularieae* and the *Hygrophoraceae*.

KEY TO THE GENERA

A Lamellae distinctly decurrent ; veil very distinctly double , spores very long
70. *Catathelasma*

A Lamellae adnexed to adnate, often sinuate, occasionally emarginate-subfree ; veil present but not always distinctly double , spores not remarkably long
71. *Armillaria*

71. **CATATHELASMA** Lovej.

Bot. Gaz. **50** : 383. 1910.

Type species : C. evanescens Lovej.

Syn. *Biannularia* G. Beck, *Pilz- und Kräuterfr.* **5** : 231. 1922.

Characters : Those of the tribus ; lamellae decurrent; spores oblong (ellipsoid oblong, ellipsoid cylindric) ; veil distinctly double. On the soil in coniferous woods.

Development of the carpophores : Hemiangiocarpous.

Area : Europe and Eastern North America, boreal in character.

Limits : Clearly separated from all other genera but evidently closest to *Armillaria* which differs in the characters indicated in the key. *Amanita* which has the same spores (amyloid and elongate in many species), bilateral trama (but of a somewhat different type of bilaterality), and double veil (though the volva usually distinctly basal), differs in the free lamellae, and, according to Kühner's data, in binucleate spores.

State of knowledge : Two of the (probably) four species have been studied thoroughly.

Practical importance : Both well known species are good edible mushrooms.

SPECIES

C. imperiale (Fr. apud Lund) Sing. (Armillaria, Quél. ; Armillariella, Konr. & Maubl. ; Biannularia, G. Beck ; Armillaria nobilis Murr.) ; *C. ventricosum* (Peck) Sing. (Lentinus, Peck ; Armillaria, Peck) ; evidently also *C. evanescens* Lovej., and most probably *Armillaria macrospora* Peck.

72. ARMILLARIA (Fr.) Quél.

Champ. Jura Vosg. p. 36. 1872 ; em. Sing., *Ann. Mycol.* 34 : 331. 1936

Type species : *A. luteovirens* (A. & S. ex Fr.) Gill.

Characters : Those of the tribus ; lamellae adnexed, even emarginate subfree or sinuate, never decurrent ; spores ellipsoid to short-ellipsoid. On the soil in frondose and coniferous woods.

Development of the carpophores : Unknown, probably hemiangiocarpous.

Area : Circumpolar.

Limits : The structure of the trama and the subhymenium separate this genus clearly from the genera of the *Leucopaxilleae ;* the presence of a veil, the structure of the trama and the subhymenium, and the less broadly attached lamellae as well as the comparatively shorter basidia separate *Armillaria* from *Neohygrophorus ;* the non free lamellae, the absence of a basal volva and the probably uninuclear (they are uninuclear in *Catathelasma imperiale* according to Kühner) spores separate *Armillaria* from *Amanita.*

This genus *Armillaria* was one of the most notoriously artificial genera of the *Agaricales* in the older classification. It was finally dismembered by Singer (*Rev. Mycol.* 5 : 10. 1940). The species of *Armillaria* in the sense of Fries and Quélet, are now distributed among the following genera : *Armillaria* sensu stricto, *Tricholoma, Calocybe, Armillariella, Melanoleuca, Leucocortinarius, Pleurotus, Catathelasma,* and *Oudemansiella.*

State of knowledge : The two species admitted here, are completely known. Several more species may enter this genus in the future.

Practical importance : The European species, *A. luteovirens,* is said to be delicious food (Emil Hermann). No other practical use is known of these species at present.

SPECIES

A. subcaligata Smith & Rea ; *A. luteovirens* (A. & S. ex Fr.) Gill. Perhaps also *Melanoleuca portolensis* Murr. (see Singer & Smith, *Pap. Mich. Ac.* 28 : 90. 1943), and probably also *Armillaria decorosa* (Peck) A. H. Smith & Walters (Tricholoma, Sacc. ; Cortinellus, Murr. ; Tricholomopsis, Sing.)

AMANITACEAE Roze

Bull. Soc. Bot. Fr. **23** : 51. 1876 (ut Amanitées, nom. nud.) ; *l. c.* p. 114 ; Heim, *Treb. Mus. Ciencies Nat. Barcelona* **15** (3) : 111. 1934.

Type genus : Amanita Pers. ex S. F. Gray.

Syn. : Pluteinées Roze, *l. c.* p. 51 (nom. nud.) ; p. 111.
Volvariaceae Roze, *l. c.* p. 51 (nom. nud.) ; p. 111 (ut Volvariées) ; Van Overeem, *Bull. Jard. Bot. Buitenzorg* **9** : 13. 1927.

Characters : Habit of the carpophores pluteoid, rarely pluteoid pleurotoid ; pigment present or absent, very different in different species as far as color and localization are concerned ; pileus often umbonate, margin often pectinate ; hymenophore in normal forms always strictly lamellate ; lamellae free or almost so (sometimes inconstantly more or less attached to the apex of the stipe, or separating, or free but fine lines running down the stipe continuing the lamellae), or at least subfree ; lamellulae becoming regularly inserted and very numerous in most species sinuate-attenuate, or suddenly truncate at a right angle (as if they were cut off) ; both lamellae and lamellulae very thin in most species ; spores more or less thin walled, amyloid or nonamyloid ; binucleate according to Kühner's data, pure white, cream color, greenish, or pink (even brownish pink) in mass, but hyaline under the microscope, with simple mostly smooth, rarely finely echinulate rough wall ; basidia normal, usually 4-spored, but there are also species or forms with constantly two spores ; cheilocystidia usually present but often very loosely attached and irregularly vesiculose ; other cystidia also often present in the pink spored genera (such as *Volvariella*, *Pluteus*, *Termitomyces*) : hymenophoral trama always bilateral at least in young carpophores, or else inverse ; stipe usually strictly central, very rarely somewhat eccentric, often veiled (annulate), and often with a volva, or with rudiments of a volva (which may also show up on the pileus) ; context sometimes with a very characteristic structure (see p. 33), nonamyloid, not heteromerous ; hyphae with or without clamp connections. On the ground in woods (often mycorrhizal but rarely selective in regard to the mycorrhizal partner), or on wood, or on termite nests, or parasitically on *Tricholomataceae*.

Limits : The family *Amanitaceae* is most likely to be confused with two other families : *Agaricaceae* and *Tricholomataceae*. As far as the former is concerned, it has formerly often been combined with the

Amanitaceae under a common tribus or family name, and in regard to the latter, the distinction was not always quite sharp.

(1) *Agaricaceae.* This family differs from the *Amanitaceae* by the structure of the hymenophoral trama which is never bilateral. Besides, the spores are most frequently of a very different type, i. e. rather thick-walled, often pseudoamyloid, or even with germ pore. The genera that have spores that would be theoretically admissable in the *Amanitaceae*, differ in several other ways — aside from the structure of the trama — e. gr. *Cystoderma* in the adnate lamellae; *Ripartitella* in the *Melanoleuca* cystidia, etc. The *Agaricaceae* are mentioned in this paragraph merely for historical reasons — not because of any actual difficulty in delimitation.

(2) *Tricholomataceae.* This family differs from the *Amanitaceae* by the trama (not bilateral or inverse) or by the broader attachment of the lamellae. However, since it is not always quite easy to draw a line between the degree of adnexedness still permissable in the *Amanitaceae* and the degree not admitted, it is fortunate that the majority of the *Tricholomataceae* has definitely non bilateral and non-inverse trama, and only one single tribus has bilateral trama. About the differences between that tribus, *Biannularieae*, and the genus *Amanita*, see under the former (p. 374-6). An important diagnostic character is also the number of nuclei in the spores at the moment of discharge, which is said to be two in the *Amanitaceae* (at least in the genera studied in this regard), and one in the *Tricholomataceae* (with few exceptions known thus far, e. gr. *Flammulina*). While it is premature to put too much emphasis on this cytological character at present, time will probably prove that the binuclear spores of the *Amanitaceae* are of some value when the position of dubious genera is considered.

As for the bilaterality of the hymenophoral trama, the author fully realizes that not all the subtypes that might be distinguished under this term are necessarily morphologically identical, nor is the inverse trama. Yet, it is demonstrated by the numerous correlated characters that all the species of this family are closely related, and since they all have either bilateral or inverse trama, it cannot be wrong to attribute some taxonomic value to it, even on the family level.

The only cases that have caused difficulties are *Termitomyces* and *Rhodotus*. *Termitomyces* was first (as *Rajapa*) placed in the *Tricholomataceae*. The reason was the age of the specimens studied. These

mens studied later, and fresh specimens studied by R. Heim clearly showed the bilateral character of the hymenophoral trama. In this case, the position of *Termitomyces* was merely a question of exact observation. In *Rhodotus*, however, the bilaterality of the trama has been observed by R. Maire many years ago, yet this exceptional species does not fit closely in any of the larger groups of the *Agaricales:* The reaction of those mycologists who have been informed of the author's intention to put *Rhodotus* in the *Amanitaceae*, has not been unanimous. In fact, the emendation of the family in order to include pleurotoid forms, is somewhat irritating. On the other hand — this still seems to be the only possible solution. The pleurotoid habit of the carpophores never goes beyond a somewhat eccentric attachment of the stipe (the stipe is even central in many cases), and the habitat on wood which is by no means unusual in the *Amanitaceae* (*Pluteus*, *Chamaeota*). The finely echinulate-rough small spores are also occasionally found in *Limacella*. In *Termitomyces*, *Chamaeota*, *Pluteus*, and *Volvariella*, even in one form of *Amanita*, the spore print is pink to brownish pink. The peculiar ornamentation of the spores, the bilateral trama, the unique structure of the epicutis of the pileus, the color of the spore print, and even the habitat on wood — all these characters taken together can scarcely find their place within any other family, than the *Amanitaceae*. The only other families where *Rhodotus* might possibly be inserted are the *Tricholomataceae*, the *Crepidotaceae*, and the *Paxillaceae*. In the *Tricholomataceae*, where *Rhodotus* has formerly been inserted, this genus is without any affinity. In a family as large as the *Tricholomataceae*, one may perhaps find a precedent for all the single characters represented in *Rhodotus*, yet the ensemble of characters is much less foreign in the *Amanitaceae* than in the *Tricholomataceae*. The *Paxillaceae* do not contain any species with pink spores, or, for that matter, with an epicutis of the structure characteristic for *Rhodotus*. In addition, a spore ornamentation of the type found in *Rhodotus* has never been observed in any genus now considered as belonging in the *Paxillaceae*. In the *Crepidotaceae*, about the same situation holds true. Here, the gelatinosity of the upper layer of the pileus of *Rhodotus* would find its most satisfactory interpretation, i. e. it would connect *Rhodotus* with the gelatinous species of *Crepidotus*. However, these gelatinous species of *Crepidotus* are so strongly different from *Rhodotus*, in the habit of the carpophores, in the color of the spore print, in the structure of the upper layer of the pileus, in the ornamentation of the spores, and even

in the septation of the hyphae — one will be forced to admit that *Rhodotus* is more affine to the *Amanitaceae* than to the *Crepidotaceae* or *Paxillaceae*. This, of course, is the situation, resulting from our present knowledge of the forms relatively most closely related to *Rhodotus*. It is quite possible that future discoveries or type studies will reveal species which are now unknown, and some of these might either confirm or contest our present views.

Phylogeny. The origin of the *Amanitaceae* is very difficult to trace. A certain similarity with the *Biannulariceae* might be explained by derivation of the *Amanitaceae* from that group. The genus *Torrendia* with its hyaline, elongate, thin-walled spores and its *Amanita* habit may also be taken into consideration. A close affinity with certain groups of the family *Agaricaceae* is also not quite impossible, and this would then link — indirectly — the *Amanitaceae* with those primitive forms that are closely related to certain of the families with colored spore print (*Coprinaceae, Bolbitiaceae*, etc.). All three hypotheses have at present their weak points — the lack of a volvate hygrophoraceous forms from which to derive the *Biannulariceae*, the lack of intermediate forms between *Torrendia* and *Amanita*; the abrupt change from bilateral to regular trama as soon as the family limits of the *Amanitaceae* are passed in the direction toward the *Agaricaceae*.

KEY TO THE TRIBUS AND GENERA

A. Spore print white, cream color or greenish, not pink to brownish pink **Amaniteae**

B. Stipe with a volva, or with rudiments of a volva, or else surface of the pileus showing distinct rudiments or fragments of the volva in the form of pyramidal or obtuse warts or flat patches of volva-tissue on top of the cuticle proper; besides, an annulus superus is potentially present, and is actually well developed in the majority of the species; clamps present or absent; spores amyloid or nonamyloid, and if nonamyloid—margin of pileus sulcate. **73. *Amanita*, p. 381**

B. Volva absent, or replaced by a glutinous covering; annulus usually present; clamp connections present; spores nonamyloid; margin not sulcate **74. *Limacella*, p. 393**

A. Spore print pink or brownish pink (rarely salmon color).

C. Spores amyloid (see *Amanita*).

C. Spores nonamyloid.

D. Hymenophoral trama bilateral; pseudorrhiza present, inserted in termite nests, or carpophore somewhat pleurotoid.

E. Cystidia none; spores subglobose, small, echinulate rough; clamp connections present; on wood in temperate zones

E. Cystidia present ; spores ellipsoid, medium sized or rather small, smooth ; clamp connections none ; on termite nest in the tropics
75. *Termitomyces* (*Amaniteae*), p. 396

D. Hymenophoral trama inverse , pseudorhiza none, at least not inserted in termite nests , carpophores not gelatinized in any organ ; sometimes growing on wood or on agarics, but never pleurotoid *Pluteeae*

F. Volva cup-shaped, always well developed.
77. *Volvariella*, p. 400

F. Volva none

G. Annulus present. 78. *Chamaeota*, p. 401

G. Annulus none. 79. *Pluteus*, p. 402

Tribus AMANITEAE Fayod

Prodrome, Ann. Sc. Nat. VII. **9** : 314. 1889 (ut Amanitacés) ; R. Maire, *Publ. Junta Cienc. Nat. Barcelona*, p. 83. 1933

Type genus : *Amanita* Pers. ex S. F. Gray.

Characters : Trama of the hymenophore bilateral.

73. AMANITA Pers. ex S. F. Gray

Nat. Arr. Brit. Pl 1 : 599. 1821.

Type species : *A. bulbosa* Schaeff. ex S. F. Gray.

Syn : *Agaricus*, trib *Amanita* (Pers ex) Fr , *Syst Mycol* **1** : 12 1821
Vaginata, Nees ex Gray *Nat Arr Brit. Pl* **1** 601 1821
Amanitopsis Roze, *Bull Soc Bot Fr.* **23** . 51. 1876.
Pseudofarinaceus O Kuntze, *Rev Gen Pl* **2** · 867 1891
Venenarius Earle, *Bull. N Y Bot Gard* **5** . 450 1909
Leucomyces Batt ex Earle, *Bull. N. Y Bot. Gard* **5** : 451 1909
Amanitella Earle, *Bull N Y Bot. Gard.* **5** : 449 1909
Lepidella Gilbert, *Bull Soc Myc Fr* **41** : 293 1925, non Van Tiegh. (1911).
Aspidella Gilbert, in Bresadola *Icon Mycol* **27** : 63. 1940
Ariella, Gilbert, *l. c.*, p. 76
Amanitaria Gilbert, *l. c.*
Amidella Gilbert, *l. c.*, p. 77.
Amplariella Gilbert, *l. c.*, p. 78.

Characters : Margin sulcate and then spores nonamyloid, or margin smooth or almost so, and then spores nonamyloid ; fragments of an at least rudimentary volva (Pl. XVIII, 2) (but in many species, volva membranous to fleshy and well developed) present either on the surface of the pileus or/and on the base of the stipe ; annulus superus

which are either sharply emarginate (as if cut off), or attenuate; lamellae free or almost so (sometimes slightly adnexed but separating in age, decurrent with a tooth which breaks off in age, or with decurrent lines at the apex of the stipe); spore print pure white, cream color, greenish, or pink (rarely so, and then spores amyloid); spores smooth, medium sized to large, thin walled, binucleate according to Kühner, globose to cylindric; basidia rather voluminous, without carminophilous granulosity, 4-spored, rarely constantly 2-spored; cystidia none, but cheilocystidia present; the latter, however, are hardly true cystidia nor are they pseudocystidia but rather fragments of the annulus superus that adhere to the edge of the lamellae when the pileus expands; hymenophoral trama bilateral with rather broad elements; stipe central; bulb at its base present or absent; context fleshy, changing or unchanging when bruised, consisting of a tissue of special structure (*Amanita* structure, see p. 33), nonamyloid; hyphae with or more frequently without clamp connections. On the ground, very rarely on other substrata, not growing from a pseudorhiza that is inserted in termite nests, usually in the forests, and often mycorrhizal.

Development of the carpophores: Hemiangiocarpous.

Area: Cosmopolitan, but the species themselves occupying definite smaller areas.

Limits: The delimitation of this genus as accepted in the present work is adequately expressed in the key, and is not in need of further elaboration. The author, like many other taxonomists, recognized the genus *Amanitopsis* as an autonomous genus, in his classification of 1936. However, the discovery of numerous African species in the Congo region by Beeli, Gilbert, and Heim throws a different light at this problem. The final proof for the generic identity of *Amanitopsis* with *Amanita* is a specimen of *A. fulva,* found near Mountain Lake, in Virginia, U.S.A., by the author in 1946. It differed from other specimens of the same species, also collected nearby, in having a distinct well developed annulus superus, exactly as *Amanita caesarea,* or *A. muscaria.* This specimen emerged from rather heavy gravelly soil, and it is possible that a higher pressure during the development of the primordia may cause annulate forms. Whatever the reason, it is now obvious that the annulate or non-annulate character of the *Amanitae* is not a generic character, and under certain circumstances not even a specific character.

State of knowledge: *Amanita* has been monographed frequently and

special attention has been paid to it by numerous mycologists and amateurs. A definite step ahead was Gilbert & Kühner's study on the amyloidity of the spores in *Amanita* (*Bull. Soc. Myc. Fr.* **44**: 149-154. 1928). It may be assumed that a further study of the macro-chemical reactions of the context and the surface of the pileus and stipe, and also of the presence or absence of clamp connections will prove to be helpful in the future. The different consistence of the volval tissue is doubtlessly an expression of the different anatomy of that organ, and further studies on this subject will also be helpful at least in achieving a more precise definition of the volval tissues. The author has found this to be true in his studies on various species from Florida, yet, the results available at present are still very incomplete.

The species from Europe and North America, and those from tropical Africa are at present best known. The data on most of the African species are taken into consideration only for supplementary indications. The main information as well as all the data for the key have been taken from material studied by the author in Europe and North America. However, even for North America, many notes on types as well as on fresh material have been set aside until more complete information on the variability of the species is available. This concerns especially regions so unusually rich in Amanitas as North and Central Florida, Alabama, etc. In the key only 46 species have been admitted. Gilbert who (1940-41) has studied many types, admits 102 species.

Practical importance: *Amanita muscaria* has been proved to be a mycorrhizal fungus. Though it is not selective in regard to its mycorrhizal partners, at least not in the manner of the boletes, it is possible that the mycorrhizal character of *A. muscaria* and other related Amanitas will eventually prove to be of some practical importance in forestry. At present, the edible and poisonous qualities of certain species of *Amanita* are economically more important than their rôle in forestry. Aside from that, *A. muscaria* is still used as fly poison in many countries in Europe and Asia, and it is also used as a drug by the inhabitants of some subarctic regions in Northern Europe, Siberia and Kamtchatka. There, dried specimens are traded extensively, and muscarin intoxication is quite common. The alcaloid responsible for these applications of the « Fly mushroom », the muscarin, is not identical with the so-called synthetic muscarin of the older chemical handbooks. The fungus product has been extracted and obtained in pure condition, during the now classical work on *Ama-*

nita muscaria by F. Kögl. He was also successful in establishing the structural formula of muscarin. This is the first complete chemical investigation of a poisonous substance in any of the poisonous agarics. The use of the « Fly mushroom » in medicine was never very extensive, and now belongs to history. Poisonings with *Amanita muscaria* are very rare since the fungus is too well known in Europe, and only the American subspecies which is more yellowish to orange, is sometimes mistaken for *Amanita caesarea* by Italian mycophagists in the Eastern United States.

Several other species of *Amanita* are even more poisonous and certainly more frequently deadly than *A. muscaria*. In fact, the most dangerous mushroom, as far as mushroom poisoning is concerned, is *A. phalloides*. It appears that it is only one out of several species (including *A. virosa*, *A. aestivalis*, *A. brunnescens*, perhaps also *A. bisporigera* and *A. verna*) containing amanita toxin, and it is often mistaken for other, edible mushrooms, such as *Tricholoma equestre*, the white forms for *Agaricus campestris*, etc. Another poisonous species is *A. pantherina* which, taxonomically, physiologically, and chemically, is closer to *A. muscaria* than to the *Phalloides* group. And finally, there are several species of *Amanita* about which no unanimous reports are available. They seem to be mildly poisonous when consumed in large quantity, or else with the percentage of poisonous matter varying in different strands, or in dependence on physiological factors unknown at present. Others were at the time not well enough known to the taxonomists themselves, and consequently, reports of their poisonous qualities cannot be relied upon, because the identification of the fungus is not quite certain. *A. agglutinata*, *A. gemmata*, *A. porphyria*, *A. chlorinosma*, *A. strobiliformis*, *A. Vittadinii*, *A. lingensis*, and *A. tainaomby* seem to belong in one of these categories.

On the other hand, many *Amanitae* are good edible mushrooms, and were known as such from antiquity. The original boletus of the Romans was *Amanita caesarea*. *A. ovoidea* was also known as excellent food in southern Europe for thousands of years. And *A. rubescens* is often indicated as being especially in demand in England. However, it is necessary to keep in mind that only an expert can distinguish the edible species from the poisonous ones, and therefore it is not surprising to see some mycophagist clubs adopting the rule of the Russian peasant who does not eat any Amanitas at all. On the other hand, wherever the edible Amanitas are well known locally, as in the

whole region from Transcaucasia to Portugal, the danger of mistaking *A. caesarea* for *A. muscaria*, or *A. ovoidea* for *A. virosa* is not very great, inasmuch as the poisonous species have a more boreal distribution, and do not seem to be so common in the area of *A. caesarea* and *A. ovoidea*.

For more specific information on the poisonous mushrooms and mushroom poisons as well as the available treatments, the reader is referred to Dujarric de la Rivière, R. & R. Heim, *Les Champignons Veneneux*, Paris 1938.

Some species contain antibiotic substances.

SPECIES

Subgenus **I. Pseudoamanita** Sing. (1936). Spores nonamyloid; margin sulcate; spore print pure white; annulus superus usually well developed or at least present in the majority of the specimens; volva either well developed and saccate, membranous, with wide free limb, or else « circumscissous » (forming belts and bands, concentric rings of warts, etc. but not entirely consisting of mealy or spiny particles); pigment usually abundant in the cuticle of the pileus, more rarely lacking; odor never of chloride of lime, not pungent at all. The poisonous species contain muscarin rather than amanitatoxin.

Type species: *A. muscaria* (L. ex Fr.) Pers. ex Gray.

Sect. 1. **CAESAREAE** Sing. (1943). Annulus and volva both constantly well developed; volva basal, membranous, with a wide saccate limb, not breaking into small verrucose fragments on the surface of the pileus; not containing any poisonous matter.

Type species: *A. caesarea* (Scop. ex Fr.) Pers. ex Schw.

A. Cokeriana Sing. (*A. recutita* sensu Coker non Fr.); *A. spreta* Peck with var. *minor* Beardslee [A. cinerea Bres. non (Otto ex Fr.) Secr.; A. spreta var. cinerea (Bres.) Gilbert; Venenarius subvirginianus Murr.]; *A. Murrilliana* Sing. (Venenarius gemmatus var. volvatus Murr.); *A. calyptratoides* Peck; *A. caesarea* (Scop ex Fr.) Pers. ex Schw.; according to Gilbert also *A. cinereoannulosa* Cleland.

African species which probably belong in this section, or are at least closely related (according to the data published by Beeli): *A. annulatovaginata* Beeli; *A. infusca* Gilbert (A. umbrina Beeli non Pers. ex Vittad.); *A. luteoflava* Beeli; *A. robusta* Beeli; *A. strobilaceovolvata* Beeli (= *Amanitopsis fibrillosa* Beeli sec. Gilbert).

Sect. 2. **MUSCARIAE** Fr. (1844 ut sect. *Amanitae*) (*Circumscissae* Quél. 1888). Annulus sometimes (usually not) and volva usually reduced; volva in belts, bands, concentric warts, or otherwise fragmentary, very rarely forming a fragile free limb and even then never cup shaped saccate; the fragments of the volva on the surface of the pileus breaking into small patches or warts; spores not quite globose; species containing muscarin (as far as this has been checked) in a larger or smaller amount (some of them so little that they are considered as edible).

Type species: A. muscaria (L. ex Fr.) Pers. ex Gray.

A. gemmata (Fr.) Gill. (A. russuloides Peck and many other synonyms); *A. Eliae* Quél.; *A. cothurnata* Atk.; *A. pantherina* (D. C. ex Fr.) Secr.; *A. muscaria* (L. ex Fr.) Pers. ex Gray with ssp. *typica*, ssp. *americana* (Lange) Sing. (A. muscaria var. americana Lange), a southeastern American geographic race (at present unnamed), and ssp. *regalis* (Fr.) Vesely (which may also be considered as an independent species); *A. Frostiana* (Peck) Sacc.; *A. parcivolvata* (Peck) Gilbert (Amanitopsis, Peck).

African species which probably belongs in this section: *A. atra* (Beeli) Sing. (Lepiota, Beeli).

Subgenus II. **Vaginaria** Forquignon (1888) [*Amanitopsis* (Roze ut genus) Barbier 1907]. Volva well developed more rarely not well developed, basal, membranous or even almost fleshy but the upper portion which is free may be very fragile and consequently not persistent; in those species with fragile volva, its fragments on the surface of the pileus often warty or pulverulent, otherwise consisting of large membranous patches, or soon washed off entirely; annulus only exceptionally present; all the temperate species edible (not containing large amounts of any poisonous matter); spores and margin as in subgenus I.

Type species: A. vaginata (Bull. ex Fr.) Quel.

Sect. 3. **VAGINATAE** (Fr. 1844) Quél. (1872) Spores globose, or nearly so.

Type species: Same as in the subgenus.

A. vaginata (Bull ex Fr.) Quel.; *A. fulva* (Schaeff. ex) Pers.; *A. crocea* Quél. apud Bourdot; *A. inaurata* Secr. [A. strangulata (Fr.) Quél. sensu Kauffman et auct. Amer., non Bres.]; *A. umbrinolutea* Secr.; *A. nivalis* Greville.

Sect. 4. **OVIGERAE** Sing. Spores distinctly ovoid to ellipsoid.

Type species: A. biovigera Sing.

A. biovigera Sing. [A. strangulata (Fr.) Quél. sensu Bres. non al.]; *A. tainaomby* Heim; *A. calopus* (Beeli) Gilbert (Amanitopsis, Beeli); *A. pubescens* Schwein.; *A. farinosa* Schw. (Amanitopsis, Atk.; Vaginata, Murr; Amanitella, Earle ex Gilbert & Kühner); perhaps *A. bingensis* (Beeli) Heim.

Subgenus III **Euamanita** Lange (1915), em. Singer (1936) [*Lepidella* (Gilbert ut genus) Vesely 1934]. Pileus non striate (sometimes « flammate », i. e. innately fibrillose or pigment in stripes, but not sulcate at the margin, or only very slightly so in very old specimens); spores amyloid; annulus mostly present; volva — if well developed — saccate and fleshy to membranous, but also often so fragile in the free portion that it leaves merely a strongly marginate bulb at the base, or sometimes entirely obliterate, either all pulverulent mealy, or not showing on the stipe (only in the warts of the pileus); pigment present or absent; odor often disagreeable or pungent, sometimes of $CaCl_2$.

Type species *A. phalloides* (Vaill. ex Fr.) Secr.

Sect. 5. **PHALLOIDEAE** (Fr. 1844) Quél. (1872) (*Volvatae* Schrot.; *Limbatae* Quél. p. p.). Spores globose or subglobose; several species of this section are deadly poisonous, containing amanitatoxin.

Type species : As in subgenus.

A. virosa Lam. ex Secr.; *A. aestivalis* Sing. (A. verna sensu aut. Amer.); *A. brunnescens* Atk.; *A. porphyria* (A. & S. ex Fr.) Secr.; *A. phalloides* (Vaill. ex Fr.) Secr.; *A. citrina* (Schaeff. ex) S. F. Gray [A. mappa (Batsch ex Fr.) Quél.]

Note : *A. suballiacea* (Murr.) Murr. and *A. maculans* (Murr.) Murr. belong to this group but may not be autonomous. *A. thejoleuca* Pat. and *A. alliiodora* Pat. also belong here according to Gilbert.

Sect. 6. **BACCATAE** Sing. ined. Spores elongate, ellipsoid to cylindric; pigment usually little; annulus sometimes wanting; flesh sometimes reddening; lamellulae either emarginate (« truncate ») or attenuate.

Type species : *A. baccata* (Fr.) Quél.

A. verna (Lam. ex Fr.) Pers. ex Vitt. sensu Arcangeli, R. Maire, Heim (Amanita ocreata Peck); *A. ovoidea* (Bull. ex Fr.) Quél. (A. alba Pers. ex Vitt.); *A. hygroscopica* Coker; *A. bisporigera* Atk.; *A. magnivelaris* Peck, *A. agglutinata* (Berk. & Curt.) Sing. [Amanitopsis, Sacc.; Amanita baccata (Fr.) Quél sensu Bresadola, Gilbert 1926 non 1941 (vix Fr.); A. curtipes Gilbert; Amanitopsis volvata (Peck) Sacc.]; *A. Peckiana* Kauffman (probably not different from

the preceding species); *A. mutabilis* Beardslee (Venenarius submutabilis Murr.); *A. cylindrispora* Beardslee.

African species which probably belong in this section: *A. subviscosa* Beeli; *A. Goossensiae* Beeli.

Sect. 7. VALIDAE Fr. (1844 ut sect. gen. *Agarici*, 1. *Amanita*) (*Incompletae* Schröt. 1889). Spores ellipsoid; pileus with blunt or low warts, rarely without warts, cuticle in most species pigmented; volva at the base of the stipe little developed; lamellulae sharply emarginate at a right angle (as if cut: «truncate»); context not reddening when exposed to the air, but sometimes slowly becoming reddish in age independently of exposure.

Type species: A. valida (Fr.) Quél. (= *A. excelsa* or *A. spissa*)

A. spissa (Fr.) Quél.; *A. excelsa* (Fr.) Quél.; *A. flavorubescens* Atk.; *A. flavoconia* Atk.; *A. rubescens* (Pers. ex Fr.) Gray (Venenarius rubens (Scop. ex) Murr.) with several varieties and forms; probably also here: *A. praegraveolens* (Murr.) Sing. (Lepiota, Murr.).

Note: A. spissa and *A. excelsa* are considered identical with each other in some recent monographic works (Vesely, Gilbert) but their taxonomic relation should be restudied; the author thought them different when collecting them and comparing them in the region east of Paris, France.

Sect. 8. STROBILIFORMES Sing. (subsect. *Strobiliforminae* Sing. 1943). Pileus white to gray, beset with large subechinate pyramidal strongly projecting angular warts from the volva; basal volva usually moderately developed (in belts); the annulus and the volva not entirely friable; spore print white or greenish; spores ellipsoid to cylindric; lamellulae emarginate («truncate») or attenuate.

Type species: A. strobiliformis (Vitt.) Quél.

A. strobiliformis (Vitt.) Quél.; *A. monticulosa* (Berk. & Curt.) Sacc. (A. Cokeri Gilbert); *A. nana* Sing.; *A. Vittadinii* (Mor.) Vitt. (Agaricus, Mor.; Lepidella, Gilbert); *A. cinereoconia* Atk.; probably also the following species cited by Gilbert for *Lepidella* but unknown to the author: *A. Atkinsoniana* Coker; *Lepidella Beillii* Beauseigneur ex Gilbert; *A. echinocephala* (Vitt.) Quél.; probably also *A. Codinae* (R. Maire) Sing. (Lepidella, R. Maire), if not identical with *A. Vittadinii*.

African species probably belonging here: *A. virella* Gilbert (A. virescens Beeli non Secr.); *A. lanosa* Beeli.

Sect. 9. ROANOKENSES Sing. Pileus white or colored; stipe white or slightly colored; both covered with friable remainders of

the volva; spore print white or slightly colored (cream, pink, greenish); annulus friable; spores ellipsoid to cylindric.

Type species : A. roanokensis Coker.

A. roanokensis Coker; *A. chlorinosma* (Peck) Sacc.; *A. Rhoadsii* (Murr.) Murr. (if really different from the preceding species).

African species probably belonging here: *A. odorata* Beeli; *A. pulverulenta* Beeli.

KEY TO THE SPECIES

A. Spores nonamyloid.
- B. Annulus present in young, well developed carpophores
  - C. Pileus orange to red under the volval fragments, or lemon yellow to pinkish buff (at least so colored when young and fresh).
    - D. Volva well developed at the base, cup-shaped saccate (if the spores are globose, see « M »).
      - E. Stipe and lamellae yellowish; pileus orange to red. *A. caesarea*
      - E. Stipe white; lamellae sometimes cream color, but more often white; pileus not orange to red but lemon yellow to pinkish buff, ochraceous to cream colored, etc.
        - F. Florida species with small stipe (less than 60 × 10 mm in an average); pileus with the color of *A. gemmata*; spores 10.7-14.5 × 6.5 – 7.2 µ. *A. Murrilliana*
        - F. California species, with larger stipe, more dull-colored pileus, and spores 9-11 × 6.5-8 µ. *A. calyptratoides*
    - D. Volva not cup-shaped or saccate but more or less broken up into a band, belts, membranous fragments, or concentric warts.
      - G. Context beneath the cuticle lemon yellow. *A. muscaria*; *A. Frostiana*
      - G. Context not pallid to yellow or pink beneath the cuticle. *A. gemmata*, *A. Eliae*
  - C. Pileus either white or gray, cream-gray, pale umber, or deep umber brown
    - H. Volva well developed, cup-shaped
      - I. Carpophores often very large; pileus covered with one large to several small patches of the volva; annulus slight, evanescent see « F ».
      - I. Carpophores small to medium sized, rarely large; pileus usually naked; annulus well developed and not fugacious. Eastern United States, or widely distributed.
        - J. Lamellae close, broad, cream color; margin slightly sulcate. Under pines. *A. Cokeriana*
        - J. Lamellae crowded, narrow, white; margin strongly sulcate; mostly under conifers. *A. spreta*
    - H. Volva not cup-shaped or saccate but more or less broken up into a band, belts, membranous fragments, or concentric warts.
      - K. Pileus predominantly white.

L. Upper margin of the bulb with a prominent obtusely rounded edge (as if provided with a ring-shaped, adnate white string); pileus predominantly white. *A. cothurnata*

L. Not so (see *A. gemmata*)

K. Pileus more or less umber. *A. pantherina*

B. Annulus none, even in early youth completely devoid of an annulus in undamaged specimens.

M. Spores globose or subglobose.

N. Lamellae with blackish edges; volva fulvous or gray, not friable, forming large coherent patches on the pileus, or none at all; in coniferous woods of Europe and Siberia. *A. umbrinolutea*

N. Lamellae rarely with brownish, mostly with white edges.

O. Volva gray, breaking into small warts on the pileus and sometimes into fragments of belts on the stipe because of the fragility of its tissue which contains a high percentage of spherocysts; both the volval fragments on the pileus and those on the stipe easily washed off by rain and by handling. Europe and North America. *A. inaurata*

O. Volva not very fragile, not gray (on the pileus either large coherent patches, or none; on the base of the stipe a persistent cup-shaped-saccate volva).

P. Pileus fulvous, copper red to bay, or buffy orange to gilvous.

Q. Pileus with a distinct orange tinge: « light ochraceous buff » with a flush of « ochraceous salmon » or « pinkish cinnamon » (Ridgway), or « Talavera » on the disc, « Gold Leaf » on margin (Maerz & Paul); phenol reaction on the context of the stipe « deep purplish vinaceous » to « Perilla purple » (R.), or « American beauty » to « Rubient » (M. & P.); circumpolar. *A. crocea*

Q. Pileus deeper fulvous to almost bay, lighter colored toward the margin but without an orange tinge; phenol reaction chocolate; circumpolar. *A. fulva*

P. Pileus gray or white.

R. Pileus gray, rarely white; stipe finely floccose, glabrescent, usually thin and fragile, soon becoming hollow; widespread. *A. vaginata*

R. Pileus white; stipe with several flocculose belts above the volva, firm and solid, very late becoming hollow. Mountains of Europe and Asia. *A. nivea*

M. Spores ovoid to ellipsoid.

S. Pileus gray.

S. Volva membranaceous; pileus not mealy

S$_1$. Volva pulverulent; pileus mealy. *A. farinosa*

S. Pileus not gray (see *A. gemmata* and several tropical African species if the volva is more or less developed at the base, otherwise *A. pubescens*, *A. parcivolvata*

A. Spores amyloid

T. Spores globose or subglobose.

U. Volval fragments on the pileus forming small areas of crusts, or friable masses, or forming rather thick warts or patches which become yellowish, green, gray, brown, or lilac, or are colored so from the beginning, or annulus gray or porphyry gray, or becoming so; context of the stipe not staining reddish chocolate color when bruised; volva not saccate, merely forming a sharp edge on a marginate bulb; mostly growing in coniferous woods near spruce and pine, or in mixed woods; moderately poisonous, or non-poisonous.

V. Pileus usually greenish pallid, citrinous-stramineous, pale sulphur color or more rarely almost white; annulus not gray, usually two annuli present, one annulus superus, another one median (a marginal veil). Circumpolar, as far as *Quercus* area reaches. *A. citrina*

V. Pileus pale porphyry gray to deep porphyry umber, or brown; annulus gray or porphyry gray, or becoming so. Circumpolar. *A. porphyria*

U. Volval fragments never colored on the pileus; annulus never gray; strongly poisonous species, containing amanitatoxin.

W. Bulb marginate with the volva not forming a free limb; context of the stipe staining reddish-chocolate color after a while when bruised; pileus and stipe large; pileus white to brown-fuliginous. North America.

X. Pileus white. *A. aestivalis*

X. Pileus brown-fuliginous, « flammate » (finely radially striped). *A. brunnescens*

W. Volva enveloping the bulb with a free membranous limb; context more or less unchanging; pileus white, or some shade of green. Europe.

Y. Pileus some shade of green; stipe subfloccose, glabrescent. *A. phalloides*

Y. Pileus pure white or almost so from the beginning; stipe usually strongly floccose all over but sometimes glabrescent; pileus campanulate and remaining so for a rather long period, usually until maturity; annulus superus often sticking to the edges of the lamellae. *P. verosa*

T. Spores ellipsoid to cylindric.

Z. Fragments of the volva on the pileus neither friable pulverulent, nor diamond-like, pyramidal and very high, but of the ordinary verrucose kind known in *A. muscaria*; volva present at the base of the stipe but only in very fragmentary pieces, or absent.

AA. Volva whitish or grayish, rarely greenish, or pale sulphur color; widely distributed species.

BB. Context not becoming reddish in age.
A. spissa, and *A. excelsa*

BB. Context becoming reddish in age. *A. rubescens*

AA. Volva distinctly deep yellow. American species.

CC. Context not becoming reddish in age. *A. flavoconia*

CC. Context becoming reddish in age. *A. flavorubescens*

Z. Pileus with friable-pulverulent volval fragments, or the volval fragments very conspicuous, diamond-shaped, or pyramidal, or coarsely spinose and high, or entirely and constantly absent, or if exceptionally present, consisting of large membranous patches.

DD. Pileus usually without any volval fragments, or if they are present, they are large, flat patches.

EE. Context not reddening when bruised.

FF. Context immediately and persistently deep and rich yellow when moistened with KOH, 15 %, watery solution, especially the cortex of the stipe of fresh and freshly dried specimens. *A. magnivelaris*

FF. Context not so reacting.

GG. Spores ellipsoid, or short-cylindric (Q of length and breadth not larger than = 2).

HH. Basidia 2-spored. North America.
A. bisporigera

HH. Basidia 4-spored.

II. Pileus thin, umbonate, soaked, moist; stipe fragile and hollow. Eastern North America. *A. hygroscopica*

II. Pileus rather thick, rather firm, exumbonate, dry to subviscid; stipe firm, solid, or eventually becoming hollow. Southern Europe, North Africa, and Western North America.

JJ. Volva soft and rather thin, white to whitish. *A. verna*

JJ. Volva firm and rather thick, ochraceous to fulvous or chestnut.
A. ovoidea

GG. Spores long-cylindric. *A. cylindrispora*

EE. Context distinctly becoming pink or reddish when bruised.

KK. Annulus constant and persistent; pileus glabrous, naked (or rarely with large, flat volva-patches); Southeastern States of the U. S. A. *A. mutabilis*

KK. Annulus obsolete, inconstant or fugacious; pileus glabrous, or more often innately squamulose-fibrillose.
A. agglutinata (cf. also *A. lepiotoides*)

DD. Pileus with high, diamond-like, pyramidal warts, or else fragments of the volva very friable and frankly pulverulent.

LL. Fragments of the volva and annulus not friable except sometimes at the margin.

MM Carpophores very small; in steppes and semi deserts of Middle Asia and India. *A. nana*

MM Carpophores of normal to very large size *A. strobiliformis, A. monticulosa, A. Vittadinii, A. cinereoconia*

LL. Fragments of the volva and annulus entirely friable-pulverulent. *A. roanokensis* and *A. chlorinosma*

74. LIMACELLA Earle

Bull. N. Y. Bot. Gard. **5**: 447. 1909.

Type species: *Agaricus delicatus* Fr.

Syn.: *Amanitella* R. Maire, *Ann. Mycol.*, **11**: 337. 1913.
Amanita subgenus *Lepiotopsis* Lange, *Dansk Bot. Ark.* **2**: 6. 1915.
Myxoderma Fayod ex Kühner (1926), Singer (1936) **
Amanita subgenus *Limacella* (Earle) Gilbert, *Le Genre Amanita Pers.*, p. 174. 1918.

Characters: Pileus more or less viscid, without fragments of a volva; epicutis consisting of variously transformed or unchanged terminal members of hyphae which are repent or ascendant or erect in a gelatinous mass; lamellae free or nearly so; lamellulae not truncate (i. e. not abruptly emarginate), spore print white; spores small, more rarely medium sized, smooth or very finely roughened to subpunctulate, hyaline, with homogeneous wall, ovoid or short-ellipsoid, or else ellipsoid to subglobose or globose; nonamyloid; basidia normal; cystidia none; aborted basidioles (pseudoparaphyses) often found on the edges; subhymenium cellular; hymenophoral trama distinctly bilateral when young, later becoming more or less irregular or intermixed; stipe dry or viscid, with a glutinous belt or cortinoid, fleshy, or membranous annulus, but without a membranous-fleshy, or pulverulent volva, always central; context fleshy; tissue nonamyloid; hyphae with clamp connections. On the ground, more rarely on decayed wood.

Development of the carpophores: Hemiangiocarpous in *L. guttata* according to Kühner, and probably hemiangiocarpous in all species.

Area: In the eastern hemisphere from Europe to Siberia and south to North Africa and the Caucasus, possibly also in South

** This genus is not actually validly published since it is an alternative for a genus previously published by Patouillard and accepted by Fayod; it does not matter that Fayod's interpretation of Patouillard's genus was erroneous.

Africa, Southern and Eastern Asia and Australia; in the western hemisphere from Canada south to Florida and Central America, possibly also in South America.

Limits: This genus differs from *Amanita* in the lack of a volva (unless the slimy coating of some species is considered as a transformed volva), in smaller spores and in the absence of the correlation, characteristic for the true Amanitas, of non amyloid spores and sulcate margin, or smooth margin and amyloid spores. It differs from all the other genera by the color of the spore print which is not pink.

Limacella is sometimes confused with other glutinous agarics, such as *Hygrophorus*, *Oudemansiella*, etc. The former has never free lamellae, and the spores are usually larger than in *Limacella* the latter has gigantic spores, basidia, and cystidia, and aside from that, regular hymenophoral trama.

State of knowledge: This genus has been studied recently by H. V. Smith as far as North American species are concerned (see *Pap. Mich. Acad. Sc.* **30**: 125. 1945). Since the American species represent the majority of the species known at present, this paper is a first step toward a monograph of the genus, and the author follows its classification.

Practical importance Some of the species, or possibly all may be mycorrhizal fungi and will perhaps become of some importance in forestry. Some are edible but they are rarely used in quantity.

SPECIES

Sect. 1. **LUBRICAE** H. V. Smith (1945, nom. nud.). Stipe viscid or glutinous.

Type species: L. illinita (Fr.) Murr.

L. glischra (Morgan) Murr.; *L. Kauffmanii* H. V. Smith; *L. floridana* (Murr.) H. V. Smith (Armillaria, Murr.); *L. oblita* (Peck) Murr.; *L. illinita* (Fr.) Murr. (Lepiota, Quél.; Amanitella, R. Maire; Amanita, Gilbert; Myxoderma, Kühner) with the varieties var. *rubescens* H. V. Smith and var. *argillacea* (Fr.) H. V. Smith; *L. roseicremea* Murr.

Sect. 2. **VISCIDAE** H. V. Smith (1945, nom. nud.). Stipe dry.

Type species: L. delicata (Fr.) Earle ex H. V. Smith.

L. roseola Murr.; *L. guttata* (Fr.) Sing. (Lepiota, Quél.; Agaricus lenticularis Lasch; Lepiota, Gillet; Amanitella, R. Maire; Amanita, Lange; Limacella, R. Maire; Agaricus Lerchei Weinmann) with var.

Fischeri (Kauffm.) Sing. (Lepiota Fischeri Kauffman); *L. solidipes* (Peck) H. V. Smith; *L. glioderma* (Fr.) R. Maire (Lepiota, Gillet; Armillaria, Quél.; Amanita, Gilbert; Amanitella, R. Maire; Melanoleuca subpessundata Murr.; Limacella, Sing.; Melanoleuca subvelata Murr.; Armillaria graveolens Murr.); *L. delicata* (Fr.) Earle ex H. V. Smith (Lepiota, Gillet; Armillaria, Boudier; Amanita, Gilbert); *L. furnacea* (Let.) Maire [L. megalopoda (Bres.) R. Maire]. — According to Konrad & Maublanc and other French authors *L. arida* (Fr.) Konr. & Maubl. and *L. Persoonii* (Fr.) Konr. & Maubl. also belong in this genus but their hymenophoral trama has not been studied.

KEY TO THE SPECIES

A. Stipe viscid or glutinous.
 B. Terminal cells of the cuticular hyphae usually 5-10 μ in diameter at the base, apices commonly attenuated. Washington . . . *L. roseicremea*
 B. Terminal cells of the cuticular hyphae usually 3-5 μ in diameter at their base; apices at times somewhat attenuate.
  C. Pileus bright yellow brown or reddish brown. North American
   D. Gluten of the stipe « burnt sienna » . . . *L. glischra*
   D. Gluten of the stipe « ocher yellow ». . . . *L. Kauffmanii*
  C. Pileus dull brown, isabelline, or white to gray or fuscous or yellowish on the disc.
   E. Pileus white to cream color, only slightly yellowish in dried material. . . . *L. illinita*
   E. Pileus differently colored.
    F. Pileus white to cream colored but gluten staining reddish, flesh with farinaceous taste. . . . *L. illinita* var. *rubescens*
    F. Pileus differently colored.
     G. Spores about 2 μ narrower than broad; lamellae forked. . . . *L. oblita*
     G. Spores rounder in outline; lamellae not forked
      H. Pileus uniformly umbrinous-isabelline; under oak in Florida. . . . *L. floridana*
      H. Pileus differently colored; under conifers in Northern Europe, Siberia, and in the West of North America. . . . *L. illinita* var. *argillacea*
A. Stipe dry
 I. Pileus rose-pink, Virginia, U. S. A. . . . *L. roseola*
 I. Pileus not so colored
  J. Annulus membranous, flaring and persistent; pileus whitish to ochraceous, alutaceous, or isabelline-flesh color, or somewhat yellowish on the disc
   K. Pileus initially colored; odor none or rancid or [illegible] or of *Tricholoma sulphureum* [illegible] lighting gas . . . *L. guttata*

K Pileus initially pure white ; odor strongly farinaceous
L. solidipes

J Annulus usually cortiniform or thick and fleshy, nor flaring, often fugacious, or ragged ; pileus usually deeper colored than indicated above.

L Pileus chestnut brown to fuliginous from a vacuolar (intracellular) pigment found in the hyphae of the gelatinized pellicle ; annulus thick ; Europe and Caucasus. *L. furnacea*

L Pileus reddish brown to fulvous, or chestnut color from an incrusting pigment on the outside of the walls of the hyphae of the hypodermium.

M Odor strong, farinaceous ; stipe 50-90 × 5-10 mm
L. glioderma

M. Odor slight, of fresh wood ; stipe 25-50 × 3-6 mm.
L. delicata

75. TERMITOMYCES Heim

Arch. Mus. Nat. Hist. Nat. ser. 6, **18** : 147. 1942.

Type species : *T. cartilagineus* (Berk.) Heim.

Syn. : Rajapa Sing., *Lloydia*, **8** : 142. 1945.

Characters : Habit of the carpophores pluteoid collybioid ; pileus with prominent umbo ; cuticle (excepting the portion on and near the umbo in certain species) consisting of repent, filamentous, hyaline hyphae ; lamellae free to subadnate-emarginate or with a decurrent tooth ; hymenophoral trama initially distinctly bilateral, then becoming regular-subintermixed in old specimens ; spore print pink ; spores nonamyloid, hyaline, ellipsoid, smooth, with continuous, homogeneous, rather thin wall ; basidia normal ; cystidia present ; stipe with a pseudorhiza and with a veil or doubly veiled, or evelate ; context compact-fleshy, or somewhat tough in the stipe ; hyphae without clamp connections, nonamyloid. The primordia developing in the holes of termite nests.

Development of the carpophores : Hemiangiocarpous according to Heim.

Area Tropics of Asia and Africa, and South Pacific.

Limits This genus can easily be separated from all other genera of agarics. Heim considered *Podabrella* Sing. as a subgenus (*Praetermitomyces* Heim) of the genus *Termitomyces*. However, in *Podabrella*, the primordia do not develop within the termite nests, and they are devoid of pseudorhiza and veil ; the epicutis of the pileus is

always and in all portions (including the umbo) a cutis rather than a trichodermial palisade or a hymeniform structure; the pigment is scanty or absent in the carpophores, and the latter are much smaller than the average size of the *Termitomyces*-carpophores. Aside from all this, it must still be proved that the hymenophoral trama of *Podabrella* is not regular. For a comparison of *Termitomyces* with similar genera, see Heim, l. c.

State of knowledge: Several species of *Termitomyces* are now well known including their individual development and their chemical characters. Heim has also studied the biological rôle of *Termitomyces* in the life of the termites, and vice versa. All these data are extremely interesting, yet, we cannot occupy ourselves with this subject in a purely taxonomic work.

Practical importance: Most species are highly valued edible mushrooms gathered by the bushel each season in Asia as well as in Africa. They are considered superior to all other mushrooms.

SPECIES

T. eurhizus (Berk.) Heim (Agaricus, Berk.; Armillaria, Sacc.; Volvaria, Petch; Collybia, Hoehnel; Rajapa, Sing.); *T. citriophyllus* Heim; *T. cartilagineus* (Berk.) Heim (Lentinus, Berk.); *T. fuliginosus* Heim; *T. striatus* (Beeli) Heim (Schulzeria, Beeli); *T. mammiformis* Heim; *T. LeTestui* (Pat.) Heim (Lepiota, Pat.); *T. Schimperi* (Pat.) Heim (Lepiota, Pat.); *T. congolensis* (Beeli) Sing. (Lepiota, Beeli); probably also *T. albuminosus* (Berk.) Heim (if specifically different).

KEY TO THE SPECIES [29]

A. Pileus grayish brown with a more or less fuliginous tinge, with more or less viscid corrugated cuticle; pseudorhiza black, at least at the base which is provided with a thick sclerotic disc; papilla acute, continuous with the profile of the pileus.

B. Fragments of the partial veil absent from the stipe.

C. Stipe hollow; lamellae lemon yellow. West Africa. ... *T. citriophyllus*

C. Stipe solid; lamellae cream color, creamy pink, or stramineous.

D. Stipe white to whitish; pileus medium sized (150 mm). Tropical Asia and Oceania. ... *T. cartilagineus*

[29] This key is based on that of Heim (l. c.) but adapted to the form used by the author, and with one species added.

D. Stipe tawny or fuliginous-brown; pileus reaching 150-200 mm in diameter. Western Africa. *T. fuliginosus*

B. Annulus membranous but not entire, nor apical, nor striate, often cobweblike. Tropical Asia and Oceania. *T. eurhizus*

A. Color of the pileus with some brownish ocher mixed in, or else not combining all the characters indicated above.

E. Papilla pointed and variable, continuous with the profile of the pileus; context reacting with pyramidon, or not.

F. Annulus none; veil reduced to cortinoid fragments or to patches on the pileus, or reduced completely.

G. Stipe solid; lamellae pinkish cream color. Equatorial Africa *T. striatus*

G. Stipe hollow; lamellae lemon yellow. Tropical West Africa (see *T. citriophyllus*)

F. Annulus apical, pendulous, striate. Tropical West Africa *T. striatus* var. *annulatus* Heim

E. Papilla abruptly individualized, conic or cylindric, blackish brown, or else carpophores very large (more than 100 mm in diameter), membranous veil always present; pyramidon not reacting with the context of the carpophores

H. Papilla poorly individualized; carpophores large, diameter of the pileus 100-125 mm. Abyssinia and East Africa.

I. Scales of the pileus due to the general veil; context without latex *T. Schimperi*

I. Scales of the pileus none; context with latex *T. Schimperi* f. *lactifluus* Heim

H. Papilla very distinct. West and Equatorial Africa.

J. Papilla cone shaped, furrowed. West Africa. *T. mammiformis*

J. Papilla cylindric, or at least not conic.

K. Pileus smooth and glabrous, almost shining. Belgian Congo and Cameroons. *T. congolensis*

K. Pileus at least uneven and opaque, often deeply rugose. West and Equatorial Africa. *T. Le Testui*

76. RHODOTUS R. Maire

Bull. Soc. Myc. Fr. 40: 308. 1925

Type species: *Rhodotus palmatus* (Bull. ex Fr.) R. Maire.

Characters: Habit pluteoid-pleurotoid; pileus with an epicutis of erect vesiculose or ampullaceous thick walled bodies which are pedicellate, the pedicels reaching downward into a gelatinized zone; lamellae free to subfree; spore print creamy pink; spores stramineous, subglobose, finely echinulate-rough, with moderately thin wall, nonamyloid, the wall homogeneous (as far as can be established considering the small size of the spores and especially the ornamen

tation); basidia normal; cystidia usually none, not even at the edge of the lamellae; hymenophoral trama distinctly bilateral when young, later less distinctly so; stipe almost central to eccentric; veil and pseudorhiza none; context hygrophanous and often watersoaked but gelatinous mainly in the immediate neighborhood of the hypodermium of the pileus, consisting of nonamyloid tissue; all hyphae with clamp connections. On dead frondose wood.

Development of the carpophores: Unknown.

Area: Europe, North Africa, Caucasus, North America; probably circumpolar.

Limits: Once it is admitted in the *Amanitaceae,* one will agree that *Rhodotus* is closest to *Limacella* and *Termitomyces.* The cuticular hyphae imbedded in a gelatinous mass, and the small, short, echinulate spores are also found in *Limacella,* and the pink spore print and often somewhat attached (instead of free) lamellae are also found in *Termitomyces.* The latter genus forms chlamydospores (see Heim, *Mem. Ac. Sc. Inst. Fr.* **64**: Pl. 7, fig. Ch. 1940, published 1941) in artificial culture (Lutz medium), and so does *Rhodotus palmatus* (see Marryat, *New Phytologist* **7**: 17. 1908). *Rhodotus* differs from *Termitomyces* in the presence of clamp connections, in the absence of a pseudorhiza and in the habitat, also in the rough spores and the gelatinous zone beneath the epicutis.

State of knowledge: The only species known has been studied repeatedly and carefully.

Practical importance: None.

SPECIES

R. palmatus (Bull. ex Fr.) R. Maire (Crepidotus, Gillet; Gymnopilus, Karst.; Pleurotus, Quél.; Gyrophila, Quél. 1888; Agaricus subpalmatus Fr.; Pleurotus, Gillet).

Tribus PLUTEEAE Fayod

Prodrome, Ann. Sc. Nat., Bot. VII, **9**: 363. 1889 (ut Pluteidés); R. Maire, *Publ. Junta Cienc. Nat. Barcelona,* 1933, p. 69, 1933 (ut Pluteae)

Type genus: Pluteus Fr.

Syn.: Agaricaceae subfam. *Volvarioideae* Imai, *Journ. Fac. Agr. Hokkaido Imp. Univ.* **43**: 153. 1938.

Hymenophoral trama inverse (Pl. XX, 2); spore print pink.

77. VOLVARIELLA Speg.

Anal. Mus. Nac. Buenos Aires 6 : 118. 1899.

Type species : *V. argentina* Speg.

Syn. *Volvaria* (Fr.) Quel., *Champ. Jura Vosg.* p. 114. 1873, non D. C. (1805).
Pseudofarinaceus Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5 : 449. 1909, non ex O. Kuntze (1891)
Volvariopsis Murr., *Mycologia* 3 : 280. 1911.

Characters : Habit of the carpophores pluteoid ; pigment present or absent ; lamellae free ; hymenophoral trama inverse ; spore print sordid pink to brownish pink ; spores smooth, nonamyloid, stramineous under the microscope, with moderately thick wall ; basidia normal ; cystidia often present ; stipe central, always with a distinct membranous volva at the base. On the soil in and outside the woods, also on wood, on decaying agarics, in hollow trunks, on straw and other vegetable matter.

Development of the carpophores : Hemiangiocarpous.

Area : Cosmopolitan, or nearly so.

Limits : The presence of a well developed volva seems to be a good character, at least in this tribus. Spegazzini intended to separate the species with « continuous » stipe in an autonomous genus, *Volvariella*. The type specimen of the type species is a true *Volvaria* in the sense of most modern authors. This means that Spegazzini's genus, if emended, can replace *Volvaria* which is a homonym.

State of knowledge : Many species have been described, yet they have never been organized into a workable monograph. The author is consequently forced to refrain from distributing the species among sections [100], and confined himself to enumerating 13 species in alphabetical order.

Practical importance : The genus *Volvariella* has as much economic importance as *Agaricus*. What the *Agaricus bisporus* culture is in

[100] R. Heim (1936) published a key to the species of *Volvaria* whereby he proposed to divide the species into three groups, *Viscosae*, *Intermediae*, and *Fibrillosae*. Heim adds that there are more groups, if tropical species are taken into consideration. It appears that these groups will in the end be some of the future sections of *Volvariella*, yet more species must be studied, and the anatomy of the various types of cuticles should be examined before these groups can be accepted as sections.

the temperate climates, that, in the tropics, is the culture of *Volvariella esculenta* and *V. diplasia*. These two species are grown in very large quantities in the Dutch East Indies, in Malaya, India, Burma, Indo-China, on the Philippine Islands and Madagascar. The methods of this culture are very crude and vary according to the availability of the substratum (usually waste products of some branch of tropical agariculture — very frequently rice straw). The fruiting bodies are sold in fresh condition in the markets.

SPECIES

V. bombycina (Pers. ex Fr.) Sing. (Volvaria, Quel.); *V. cnemidophora* (Mont.) Sing. (Volvaria, Sacc.); *V. diplasia* (Berk. & Br.) Sing. (Volvaria, Sacc.); *V. esculenta* (Mass.) Sing. (Volvaria, Mass.); *V. media* (Schum. ex Fr.) Sing. (Volvaria, Gillet); *V. plumulosa* (Lasch ex Oudemans) Sing. (Volvaria, Quél.); *V. pubescentipes* (Peck.) Sing. (Volvaria, Sacc.; Volvariopsis, Murr.); *V. pusilla* (Pers. ex Fr.) Sing. (Volvaria, Quél.); *V. speciosa* (Fr.) Sing. (Volvaria, Gillet) and its variety var. *gloiocephala* (D. C. ex Fr.) Sing. (Volvaria gloiocephala, Gillet); *V. surrecta* (Knapp) Sing. [Volvaria, Ramsbottom; V. Loveiana (Berk.) Gillet]; *V. Taylori* (Berk.) Sing. (Volvaria, Quél.); *V. villosovolva* (Lloyd) Sing. (Volvaria, Lloyd); *V. volvacea* (Bull. ex Fr.) Sing. [Volvaria, Quél.; Volvaria virgata (Pers.) Quél.].

78. CHAMAEOTA (W. G. Smith) Earle

Bull. N. Y. Bot. Gard. **5**: 446. 1909

Type species : Agaricus xanthogrammus Ces.

Syn.: *Agaricus* subgenus *Chamaeota* W. G. Smith, *Clavis Agar.*, p. 15. 1870.
Annularia (Schulz.) Gillet, *Champ. Fr.*, p. 389. 1876, non Sternb. (1823), nec Hochst. (1841).
Agaricus subgen. *Annularia* Schulzer. *Verh. Zool. Bot. Ges. Wien* **16**: 49. 1866.

Characters. As in *Volvariella*, but without a volva; annulus present; spore print between « Paloma » and « Sonora ». On wood, rarely on the earth in woods.

Development of the carpophores: Unknown.

Area: Probably cosmopolitan (except for the frigid zones).

Limits : This genus differs from both *Volvariella* and *Pluteus* (and perhaps *Metraria*) merely in the characters of the veil. It is impossible to tell at present whether, in this particular case, a distinction of a genus from two or three others on the basis of velar characters will prove to be artificial as it has been proved to be in several other cases. On the other hand, the distinction of the genus *Chamaeota* by the presence of the annulus cannot be rejected a priori, and its delimitation is extremely simple and convenient on the basis of the present diagnosis. There is little likelihood that *Chamaeota* will be given up lightly, unless strong reasons can be given to support its supression.

Under present circumstances, we may say that all species of *Chamaeota* are at least partly yellow ; the hyphae of the epicutis are cylindric-filamentous as in sect. *Trichoderma* Fay. of *Pluteus*, and the septa are clampless. The group of species thus circumscribed, is very homogeneous and natural. On the other hand, species with pseudoamyloid spores, with germ pore, or with a distinct metachromatism in cresyl blue cannot be considered as belonging in *Chamaeota ;* they all have regular rather than inverse trama, and are here referred to the *Agaricaceae.*

State of knowledge : The type species is incompletely known. No specimens have been available to any modern author, and the description given by Cesati has not been emended. However, the diagnosis as published originally by Cesati is fully correct for a species of *Chamaeota*, and his guess at *Pluteus* is very significant. It is conceivable that Cesati confused some species of the family *Agaricaceae* but the thin stipe does not favor this interpretation. Consequently, no immediate danger to the generic name *Chamaeota* can be seen. If type specimens of Cesati's species should be found to be in disagreement with generic diagnosis given above, it would not be advisable to rush for a nomen novum since it is quite possible that *Chamaeota* would actually better be included in *Volvariella* or *Pluteus* – a problem that only more intensive monographic studies on both genera can solve. The two American species are the only well known species in the genus *Chamaeota.*

Practical importance : None.

SPECIES

C. sphaerospora (Peck) Kauffm. (Annularia, Peck); *C. mammillata* (Longyear) Murr. (Annularia, Longyear); evidently also *Annularia Fenzlii* (Schulzer) Gillet and an undescribed species from the Caucasus (see Singer 1929). The two American species may be conspecific with each other, or even with *A. Fenzlii*.

79. PLUTEUS Fr.

Genera Hymen. p. 6. 1836.

Type species : *Agaricus pluteus* Batsch ex Fr., synonymis exclusis (= *Pluteus cervinus*).

Syn.: *Rhodosporus* Schröter in Cohn, *Krypt.-Fl. Schlesien*, p. 617. 1885-89.

Characters : Habit of the carpophores pluteoid; pileus with hymeniform, or cellular epicutis, or the hyphae of the epicutis filamentous, allantoid, or cylindric fusoid and not hymeniform; lamellae free; spores usually ovoid or (short) ellipsoid, more rarely subcylindric or globose, with moderately thin, smooth, nonamyloid, stramineous, homogeneous wall, usually rather small to medium, rarely rather large; basidia normal; cystidia often present, sometimes with characteristic hooks (Pl. XXII, 4), in other species only cheilocystidia present; hymenophoral trama inverse; stipe central, usually fleshy-subfibrillose; context of the pileus most frequently white, consisting of fleshy, nonamyloid tissue; hyphae with or without clamp connections; on various substrata, on dead and living plant tissue, on humus and sand, but most frequently on decayed wood in the forests.

Development of the carpophores : Unknown, at least in detail for all species except *P. admirabilis* which is pseudoangiocarpous according to the data published by Walker.

Area : Definitely cosmopolitan.

Limits : *Pluteus* is not close to any other genus except for *Chamaeota*.

State of knowledge : This genus is comparatively well studied in Europe, yet a good, even regional, monograph has not been published. In North America, many more species than in Europe have been described, and most of them have not yet been studied

anatomically; we know almost nothing about the structure of the epicutis which is of primary importance, and we also know nothing about the presence of the clamp connections in most of these species. Even the cystidia, which have been used for taxonomic purposes in this genus by many authors, have been given little attention in such works as *North America Flora*. It is therefore impossible to write a conspectus of the temperate species not to mention those of tropical Africa, Asia, Australia, or South America. The number of species described until 1925 was 132. More species have been described since then. Some of them are synonyms, yet, new species are still being described from regions that are generally believed to be well explored. The author admits 28 species.

Practical importance: In spite of the excellent culinary qualities of some of the *Plutei*, representatives of this genus are rarely found in the markets, and are also rarely used by amateurs. The wood-destroying properties of some species are limited to previously decayed, dead wood, or at least dead tissue on living trees; this, however, is valid only for the most common species, and exceptions will probably be found. It is highly improbable that *Pluteus* counts among the true mycorrhiza-fungi.

SPECIES

Sect. I. **TRICHODERMA** Fayod (1889) (*Tricholomatae* Lange 1917, *Fibrillosi* Imai 1938). Epicutis fibrillose, i. e. consisting of elongate hyphae, and not arranged in a hymenium, but sometimes with bunches of cystidioid erect bodies.

Type species: P. cervinus (Schaeff. ex Secr.) Fr.

P. roseipes Hoehn.; *P. tomentosulus* (Peck) Peck; *P. cervinus* (Schaeff. ex Secr.) Quél.; *P. petasatus* (Fr.) Karst.; *P. salicinus* (Pers. ex Secr.) Quél.; *P. atromarginatus* (Sing.) Kühner (P. cervinus var. atromarginatus Sing.); *P. Roberti* (Fr.) Gillet sensu Lange non Ricken; *P. hispidulus* (Fr.) Quél.; *P. plautus* (Weinm.) Gillet; *P. umbrosus* (Pers. ex Fr.) Quél. sensu Ricken non Quél. nec Boudier, nec Bres.; *P. cinereus* Quél.; *P. sororiatus* (Karst.) Karst.; *P. luteomarginatus* Rolland; *P. nigrolineatus* Murr. (which is perhaps nearly identical with C. cyanopus Quél. sensu Bres., Lange); *P. leoninus* (Schaeff. ex Fr.) Quél. sensu Sing.; *P. Bruchii* (Speg.) Sing. (Nolanea, Speg., if not too close to the preceding species); *P. alborubellus* (Mont.) Pat. sensu Pat.

Sect. 2. CELLULODERMA Fayod (1889). (*Micaceae* Lange 1917, *Pruinosi* Imai 1938). Epicutis hymeniform or consisting of sphero-cysts (forming an epithelium).

Type species: *P. nanus* (Pers. ex Fr.) Quél.

P. nanus (Pers. ex Fr.) Quél. with several forms and varieties, e. gr. var. *lutescens*, and probably also the « species » *P. cinereofuscus* Lange, *P. alachuanus* Murr. and *P. umbrinellus* (Sommerfeldt) Gillet; *P. cyanopus* Quél. sensu Métrod non al. (an Quél.?); *P. eugraptus* (Berk. & Br.) Sacc.; *P. chrysophaeus* (Schaeff. ex Lasch) Quél.; *P. glyphidatus* (Berk. & Br.) Sacc. (if not too close to the preceding species); *P. Kesslerii* Sing.; *P. semibulbosus* (Lasch) Gillet; *P. longistriatus* (Peck) Sacc.; *P. admirabilis* (Peck) Peck; *P. coccineus* (Cooke) Mass. (P. caloceps Atk.); *P. xylophilus* (Speg.) Sing. (Entoloma, Speg.).

KEY TO THE SPECIES

The American species and the few non-European species added to this list of European species and incorporated in the conspectus above do not justify the writing of a new, revised key. The European species can be determined by the use of Lange's (*Flora Agaricina Danica* **2**: 81-82, 1936) key if some additional literature is consulted.

GENERA INCOMPLETELY KNOWN

Metraria Cooke & Mass. apud Sacc. **9**: 82. 1891. « Stipe central; volva and annulus distinct; pileus fleshy; spores flesh color. Analogous with the genus *Amanita* ». Saccardo. The type species is *M. insignis* Cooke & Mass. apud Sacc. In spite of various attempts to find a specimen among Massee's collections at the New York Botanical Garden, New York, United States, or at the Kew Herbarium in England, the author was unsuccessful in securing authentic material. The species is described from Australia where it is said to grow on the earth. While there is no reason to doubt the existence of a genus or group in the *Pluteeae* where an annulus and a volva are found in the same carpophore, as they are in *Amanita*, it may well be that *Metraria* is a genus without any affinity to the *Pluteeae*. As long as it is not known what tramal structure, what spores, cystidia (if any) and epicuticular structure the original *Metraria* has, it is impossible to recognize *Metraria* on the same level as *Pluteus*, *Volvariella*, etc. (Cf. also Gilbert, 1941, p. 248).

Volvella Gilbert & Beeli apud Gilbert. *Notules sur les Amanites*

(Supplement), p. 3. 1941. « Carpophores volvate, pileate and stipitate; flesh changing; pileus ...with smooth margin; cuticle colored, beset with colored floccons; stipe annulate, ...; annulus membranous, persistent; volva membranous, saccate, persistent; hymenophore lamellate; lamellae free, initially white; ...spores nonamyloid, smooth, hyaline, ellipsoid, small ». The type species is *V. floccosolivida* (Beeli) Gilbert & Beeli, a species from the Congo, painted by Goosens and published in Beeli, *Flore Iconographique Champ. Congo*, p. 16, pl. 1, fig. 9. 1935 under the name *Amanita floccosolivida* Beeli. Gilbert assumes that the spore print is ochroleucous, but has seen no print. The wall of the spores is said to be rather thick, citrinous or pale ochraceous under the microscope. Gilbert neglected to publish on his findings regarding the structure of the hymenophoral trama — if the latter was studied at all. Without an indication on this important character, the genus *Volvella* cannot be recognized on the same level as *Amanita*, or *Volvariella*.

AGARICACEAE Fr.

Syst. Orb. Veg., p. 65. 1825 (ut « subordo » Agaricini [illegible]), Chev., *Flore Paris* 1 : 121. 1826 (ut « ordre » *Agariceae*); Cohn, *Hedwigia* 11 : 17. 1872 (ut fam. *Agaricaceae*); em.

Type genus : Agaricus L. ex Fr.

Syn.: *Agariciformes* Schwein., *Schr. Naturf. Ges. Leipzig* 1 : 78. 1822 [illegible]. *Lepiotaceae* Roze, *Bull. Soc. Bot. Fr.* 23 : 51. 1876 (nom. nud.), *l. c.*, p. 111 (ut Lépiotées); Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9 : 19. 1927.

[illegible] Neither the designation as subordo, nor the spelling of the ending invalidates the status of Fries' family in the author's opinion. Since there was no such status as families in the scheme used by Fries in *Systema Mycologicum*, or in *Systema Orbis Vegetabilis*, it is obvious that the taxon above the genus is meant to take the place of the modern family conception. Since this group was proposed long before it became customary to form family names in the fungi with the suffix -aceae, and even longer before the International Rules recommended to do so, it is not unexpected to find Fries' name formed in a different way. If we would not interpret the rules somewhat liberally in this particular case, i. e. when admitting family names that were not originally designated as families, or had not the accepted ending, we would undoubtedly find ourselves in nomenclatorial difficulties even more annoying than those we have to face at present.

[illegible] This is the oldest family name for the group under consideration; however, since it is not formed from a generic name as required in the International Rules, Art. 23, it cannot be accepted.

Psalliotées Roze, *l. c.*, p. 51 (nom. nud.); p. 113.
Polyphylles Quél., *Enchiridion*, p. 2. 1886 (lectotype: *Agaricus* L. ex Fr.), p. p.
Leucocoprinaceae Sing., *Ann. Mycol.* **34**: 323. 1936 nom. subnud.

Characters: Habit of the carpophores tricholomatoid or collybioid, or most frequently pluteoid, but usually showing a very characteristic appearance of its own because of the furfuraceous to scaly surface (often with a smooth disc, « calotte ») and the annular veil; pileus often umbonate; epicutis consisting most frequently of a palisade (trichodermial palisade), but also often hymeniform, or forming an epithelium, or consisting of parallel, repent hyphae (cutis), or else consisting of repent, interwoven hyphae which surround single spherocysts (heteromerous); hymenophore lamellate [103]; lamellae thin, free, or more rarely adnexed, adnate or decurrent; hymenophoral trama regular to irregular but never truly intermixed, and never bilateral, and also never inverse; basidia normal, i. e. without carminophilous granulosity and comparatively rather small, mostly 4-spored; cystidia present or absent; spore print most variable, pure white, cream color, ochraceous, green to olive, pink, purple, or sepia, sometimes changing color by dehydration (especially from green to purple); spores under the microscope hyaline to stramineous, or brownish, bay, or melleous, smooth or echinate, warty, punctate, echinulate-rough, etc., with comparatively thick simple wall or with complex wall and then rather thick-walled, to very thick-walled, with or without germ pore, with or without a metachromatic (in cresyl blue) endosporium, with or without a persistent perisporium, amyloid, or nonamyloid, or most frequently from slightly to very strongly pseudoamyloid, usually binucleate, very rarely uninucleate (according to Kühner); stipe central, often remote from the hymenophore by a collarium, often with a more fibrous structure than the soft fleshy pileus, and then easily separable from the latter, with a membranous or cortinoid (usually membranous and funnel shaped) veil which is in most cases, at least partly, a marginal veil, and in some genera becomes movable very early; volva also present, or rudimentary, or completely absent; context fleshy, consisting of amyloid or much more frequently nonamyloid hyphae with or without clamp connections. Pileus and context

[103] Rick (in litt.) indicates a rare poroid (gastroid ?) aberration of the hymenophore of an *Agaricus* sp. in Brazil (= *Boletus albidus* (Romagnoli) Mre).

often strongly reacting (deep and rapid color reactions) with the usual reagents. Most frequently on the earth or on sand or humus in woods, but also on various dead or living plant tissues (*Pterydophyta*, wood of conifers, and *Angiospermae*), also in deep moss; very frequently in greenhouses, steppes and deserts, often in fields and sand dunes.

Limits: The *Agaricaceae* are somewhat intermediate between the group of families treated up to this point (*Hygrophoraceae*, *Tricholomataceae*, *Amanitaceae*) on one hand, and the dark spored agarics (*Coprinaceae*, *Bolbitiaceae*, *Strophariaceae*) on the other hand. There is also some difficulty in the separation of the *Agaricaceae* from the *Cortinariaceae* because of the genus *Phaeolepiota*.

(1) *Amanitaceae.* Among the light spored groups, the *Agaricaceae* are most similar to the *Amanitaceae*. However, the spores of the *Amanitaceae* are usually distinctly different, having thin, simple, amyloid or nonamyloid (never pseudoamyloid) uninterrupted walls, and, more important, the hymenophoral trama is always bilateral or inverse.

(2) *Coprinaceae.* Among the dark-spored groups, the *Agaricaceae* come closest to the *Coprinaceae*. The genus *Cystoagaricus*, being dark-spored and provided with an epithelium at the same time, can be separated from the *Coprinaceae* only by the correlation of the following characters: The free lamellae, the small basidia, the angular or subangular spores; the vesiculose, septate cheilocystidia, and the hymenophore of the aequihymeniiferous type. The genus *Macrometrula*, on the other hand, having a volva and subfree lamellae, reminds one of certain volvate *Agaricaceae*, such as *Clarkeinda*, but, in the autor's opinion, it is merely a volvate representative of the *Psathyrella* series, not a genus of the *Agaricaceae*. It has the characteristic cheilocystidia and the characteristic structure of the cuticle of the Psathyrellas. The separation of the *Agaricaceae* from the *Coprinaceae* must therefore be realized in such a way as to leave *Cystoagaricus* with the *Agaricaceae*, and *Macrometrula* with the *Coprinaceae*.

(3) *Strophariaceae.* A small, little known group of species intermediate between *Agaricus* and *Strophoria* (in the broader sense) connects the families *Agaricaceae* and *Strophariaceae*. These species are American species, one described as *Stropharia Kauffmanii*, and the other still undescribed. They remind one very much of certain Pholiotas such as *P. squarrosa* but they do not have any chrysocystidia, and their lamellae are very narrowly adnexed to almost free. They differ from *Agaricus* in a different type of cheilocystidia

and probably also in the chemical reactions, as well as in the attachment of the lamellae to the stipe; they differ from *Stropharia* and *Naematoloma* in the absence of chrysocystidia, and from *Psilocybe* in the narrowly attached to subfree lamellae, the squamose or squarrose pileus, and the small spores. Further studies will decide whether this group is closer to *Agaricus*, or to the *Strophariaceae*, and in the latter case, whether or not it is necessary to base a new genus on these species. If they are temporarily left out of consideration, the distinction of the *Agaricaceae* from the *Strophariaceae* is easy insofar as all the species with colored spores have definitely free lamellae in the *Agaricaceae* unless they are covered with an epithelium all over the pileus and stipe; in the *Strophariaceae*, on the other hand, the lamellae are always strongly attached, broadly adnexed (with or without sinuation), adnate or even decurrent, and an epithelium is never present.

(4) *Cortinariaceae*. This family is very different from the *Agaricaceae* excepting one link—*Phaeolepiota*. *Phaeolepiota* can be interpreted as an ochrosporous *Cystoderma*. In fact, the characters of all organs excepting the spores, agree perfectly in both genera, *Cystoderma* and *Phaeolepiota*, and certain large American species of *Cystoderma* look so much like *Phaeolepiota aurea* that they can easily be mistaken for it in the field. On the other hand, *Phaeolepiota* often shows rather distinctly punctate spores and a strong perisporium; the spores are distinctly colored under the microscope and the genus could also be considered as close to *Phaeomarasmius* and *Naucoria*. In the latter genus, there are species with a similar covering of the pileus, only smaller in size.

The author has finally decided in favor of the *Agaricaceae*, for the following reasons: The affinity of *Phaeolepiota* with *Cystoderma* is more obvious and more probable than that with *Naucoria*. The ochraceous spores are not unexpected in a family which is so remarkable for the variability of the spore print within a single genus such as *Lepiota* and *Leucoagaricus*. The punctation of the spores is similar to that observed in the genus *Melanophyllum* which is a true representative of the *Agaricaceae*, and so close to *Lepiota* that it has been considered as a species of the latter genus by many taxonomists up to very recently. A well developed and somewhat persistent perisporium is often found in species of the *Agaricaceae*, and generally speaking has not much taxonomic value on the generic or family level. Roger Heim and A. H. Smith have recently expressed their

belief that *Phaeolepiota* is close to *Cystoderma*. The author therefore feels that the innovation suggested by transferring the genus *Phaeolepiota* to the *Agaricaceae* is not a surprise, nor the isolated opinion of a single mycologist.

Phylogeny : The family *Agaricaceae* may have derived from gastromycetous ancesters. It may, however, be supposed that this derivation is at least not a direct one, whereby the evolutionary series would pass through the families *Coprinaceae*, *Bolbitiaceae*, or else, perhaps through the *Amanitaceae*. The latter question can be decided only when it becomes reasonably certain that the spores have been pale and hyaline at first and have phylogenetically developed to deep-colored, or vice versa. The author is inclined to think that the immediate ancesters of the *Agaricaceae* are gastromycetous, and that the similarity with the *Amanitaceae* is external rather than caused by affinity, and the similarity with certain dark spored agarics can be explained by the fact that they derive from similar *Gastromycetes* by a similar process of transformation.

KEY TO THE TRIBUS

A. Spores pseudoamyloid ; endosporium metachromatic in cresyl blue, or germ pore very broad and conspicuous ; spore print never brownish-purple (not even by dehydration) ; lamellae quite free, often remote from the stipe by a collarium. *Leucocoprineae*, p. 411.

A. Spores pseudoamyloid, or amyloid, or nonamyloid ; germ pore present or absent (if present — spore print brownish-purple or sepia, at least in dehydrated condition) : endosporium not metachromatic in cresyl blue ; lamellae free or attached.

B. (*) Spores more or less pseudoamyloid, rarely amyloid, rarely brownish-purple (not becoming so in dehydrated prints) ; lamellae free. *Lepioteae*, p. 436

B. Spores either completely nonamyloid, or brown spore wall pigment hindering the observation of pseudoamyloid reaction in most cases, or lamellae not free.

C. Spore print brownish-purple (at least through dehydration), or sepia, often green when fresh. *Agariceae*, p. 427

C. Spore print not as above *Cystodermateae*, p. 444

(*) If trama composed of conducting elements and staining yellow and epicatenular layer a cutis, see also genus *Phlebonema*

Tribus LEUCOCOPRINEAE Sing.

Pap. Mich. Ac. Sc. **32**: 141. 1946 (publ. 1948)

Type genus: Leucocoprinus Pat.

Characters: Spores with complex walls and germ pore, pseudoamyloid, completely deep blue in cresyl blue, or distinctly metachromatic in cresyl blue (mostly the latter), and then spore print usually pure white or cream color or pink; volva not well developed and often rudimentary, or well developed (*Clarkeinda* and *Lepiotella*), or none.

Note: This tribus corresponds to the genus *Leucocoprinus* in the sense of Locquin.

KEY TO THE GENERA

A. Spore print green or olive when fresh; flesh often reddening when wounded
  B. Volva distinct; spores small. 80. *Clarkeinda*
  B'. Volva none; spores medium to large 81. *Chlorophyllum*
A'. Spore print neither green nor olive when fresh
  C. Clamp connections present.
    D. Pileus scaly (not merely excoriate, or furfuraceous) with usually distinctly palisadic structure on the disc (calotte), fleshy and not fragile, not at all plicate-sulcate, never bright yellow 82. *Macrolepiota*.
    D'. Not showing any of these characters (see *Leucocoprinus*)
  C'. Clamp connections absent.
    E. Pileus scaly; spore print « colonial buff »; context reddening; stipe long, with movable annulus; spores 10-13 μ long, becoming uniformly deep blue in cresyl blue (see *Chlorophyllum*).
    E'. Not combining the characters indicated above
      F. Epicutis of pileus not consisting of spherocysts unless margin sulcate; veil usually distinct.
        G. Pileus fleshy and thick, at least in the larger part of the radius (extreme margin may be thin and sulcate), not long-plicate-sulcate; context often changing on exposure (red, yellow); pileus not covered with spherocysts; stipe comparatively short; basidia monomorphous; gills marbled in iodine 83. *Leucoagaricus*.
        G'. Pileus with very thin context, radially plicate or sulcate; context usually unchanging; pileus sometimes covered with spherocysts; stipe often subfilamentous and long; hymenium of the *Psathyrella* sub-type (according to Buller) 84. *Leucocoprinus*.
      F'. Epicutis of pileus consisting of spherocysts; margin not sulcate, annular veil poorly developed (cf. *Schulzeria flavidula* Rick sensu Sing., see p. 444)

80. CLARKEINDA O. Kuntze

Rev. Gen. Pl. **2**: 848. 1891.

Type species: C. poderes (Berk. & Br.) O. Kuntze.

Syn *Chitonia* (Fr.) Karst., *Bidr. Finl. Nat. Folk* **32**: 274. 1879, non aut. prior.
Agaricus subgen. *Chitonia* Fr., *Hymen. Eur.*, p. 287. 1874
Chitoniella Mass., *Brit. Fung. Fl.* **1**: 418. 1892 (hyponymous) [125]
Chitoniella Henn. in Engler & Prantl, *Nat. Pfl.-Fam.*, I. **1****: 240. 1898
Chitonis Clements, *Gen. Fungi*, p. 114. 1909

Characters: Pileus usually scaly, fleshy; spore print green to olive when fresh (darkening by dehydration?); spores rather small (much less than 10 μ long), with distinct germ pore, with compound wall, smooth, pseudoamyloid, metachromatic in cresyl blue (?); cystidia none on the sides of the lamellae; cheilocystidia present; hymenophoral trama rather regular at first, becoming irregular; annulus usually complex, movable; volva basal, cup shaped, firm, persistent and never anuliform. On the ground.

Development of the carpophores: Obviously hemiangiocarpous.

Area: Tropical Asia.

Limits: This genus is evidently closest to *Chlorophyllum*, and some authors will prefer to consider these genera as synonyms whereby *Clarkeinda* would emerge as the valid name. However, there are several important characters separating *Chlorophyllum* and *Clarkeinda*, among them the smaller spores, and the volva of *Clarkeinda*. Boedijn, in fact, thinks that *Clarkeinda* is closer to *Agaricus* whereas *Chlorophyllum* is closer to *Lepiota* (what he has in mind, is *Macrole-*

[125] It is difficult to decide whether Massee's genus should be considered as validly published. He says: « ... to be consistent, the genus *Chitonia* Fries including both ringed and ringless species, must be divided into two genera, *Chitonia* including the species without ring, and the species furnished with a ring included in a genus that might be called *Chitoniella* ». The only species indicated by Massee for *Chitonia* is *C. rubriceps*, now considered as the type species of the genus *Macrometrula*. The true Chitonias (= *Clarkeinda*) are either annulate or exannulate. If Massee actually proposed a new genus (the words « might be called » do not suggest it) in the text quoted above, it is still doubtful whether he considered as the type of the emended *Chitonia* his *C. rubriceps*, or one of Fries' exannulated Chitonias. In the first case, his attitude would not be conform with the type method; therefore, the other alternative is assumed to be true. Consequently, *Chitonia* and *Chitoniella* in Massee's sense are here considered to be congeneric and identical, and synonymous with *Clarkeinda*.

piota). The author believes that a final solution can be proposed only after a few points in the diagnosis of *Clarkeinda* are completely cleared up. These are (1) the color of the spore print after desiccation, (2) the presence or absence of clamp connections, (3) the metachromatism in cresyl blue. The author has attempted to study the type but the type specimens are all completely immature and there are so few spores — and these are immature — that the metachromatism observed should be noted with some skepticism for the time being; the material did not reveal clamp conections, but is was not enough and not in good enough condition for anatomical study to exclude the possibility of irregular occurrence of clamp connections. The color of the spore print is indicated as green or olive by Boedijn as well as by Petch, the only authors who have published on this fungus from detailed personal knowledge of the fresh fungus. The indications of purple brown spores may be based on a discoloration phenomenon comparable to what is known in *Melanophyllum*, or else it may be based on imprints of the lamellae on white paper caused by the autoxidation (the flesh reddens when touched) of the cell sap. In the latter case — and this alternative appears to be more probable — the indication of purple brown spores must be considered as a plain misstatement. If, in the end, all these questions are answered in a way to suggest identity of these characters in both *Chlorophyllum* and *Clarkeinda*, the problem of separation will indeed become a difficult one.

Otherwise, this genus is well separated from all other agarics, in the tribus *Leucocoprineae* as well as in other groups.

State of knowledge : The work previously done on the only representative of this genus by Petch, Boedijn, and Singer makes it absolutely certain that *Clarkeinda* belongs in the *Agaricaceae*, and is closest to *Chlorophyllum*. On the information still lacking, see the preceding paragraph.

Practical importance : None.

SPECIES

C. trachodes (Berk.) Sing. (Agaricus, Berk.; Chitoniella, Petch; Agaricus pedilia Berk. & Br.; Chitonia, Sacc.; Clarkeinda, O. Kuntze; Agaricus poderes Berk. & Br.; Chitonia, Sacc.; Clarkeinda, O. Kuntze; Chitoniella, Henn.).

81. CHLOROPHYLLUM Massee

Kew Bull. for **1898**, 135. 1898.

Type species: *C. esculentum* Mass. [*C. molybdites* (Meyer ex Fr.) Mass.].

Characters: Those of the tribus; habit of the carpophores similar to that of the species of *Macrolepiota*; pileus scaly; epicutis consisting of a palisade of erect hyphae on the disc, the palisade soon broken and fasciculate-twisted on the margin, or disappearing from the margin inward; lamellae usually becoming green in age, quite free and remote from the stipe; spore print green (various shades, not constant [101]), or more rarely « colonial buff » (Ridgway); spores smooth with thick, complex wall and colorable with cresyl blue in all their parts (therefore indistinctly metachromatic in fresh or recently dried material), with broad germ pore, with an intermembranal space visible in phloxine mounts, large; cystidia none on the sides of the lamellae; cheilocystidia present; hymenophoral trama almost regular becoming irregular with age; stipe elegante (longer than the diameter of the stipe in most individual carpophores), with a bulb at the base, without a cup-shaped volva, with movable annulus which is somewhat fixed in youth but becomes free on drying, and is complex as in *Macrolepiota*; context inclined to redden when bruised, containing a poisonous matter; hyphae nonamyloid, without clamp connections. Mostly on rich soil.

Development of the carpophores: Hemiangiocarpous.

Area: Tropical America, Oceania, Asia, north to North America (New York and Michigan), south to Buenos Aires.

Limits: See under *Macrolepiota*, *Leucoagaricus*, and *Clarkeinda*.

State of knowledge: A complete study of this species has been made by Singer (*Mich. Ac. Sc. Pap.* **32**: 137. 1947). It will probably be possible to distinguish several races whithin this species according to the intensity of the reddening, the exact tone of the spore print, perhaps also according to physiological characters, such as the amount of poisonous matter present in the fruiting bodies. It is improbable, however, that these characters will coincide with

[101] The spore print of the original material on which *Lepiota Morgani* Peck was based, is now preserved at the Farlow Herbarium, and has faded to « powdered gold » (Maerz & Paul).

geographic races since there is an abundance of variation at a single locality.

Practical importance : This species is poisonous in North America and the Philippines. It has been reported as edible in South America in one instance, but this indication must be accepted with caution.

SPECIES

C. molybdites (Meyer ex Fr.) Mass. [Læucocoprinus, Pat. ; Lepiota, Sacc. ; Agaricus guadelupensis Pat. ; Lepiota Morgani (Peck) Sacc.].

82. MACROLEPIOTA Sing.

Pap. Mich. Acad. Sc. **32** : 141. 1946 (publ. 1948).

Type species : M. procera (Scop. ex Fr.) Sing.

Syn. : Leucocoprinus subgenus *Eu-Leucocoprinus* Locquin, *Bull. Soc. Linn. Lyon* **14** : 80. 1945.

Characters : Those of the tribus; spore print pure white in all species known; spores distinctly and strongly metachromatic in cresyl blue, and not uniformly deep blue under any circumstances, with a broad germ pore, smooth, very voluminous (above 10 μ in length and sometimes reaching 25 μ); cystidia none on the sides of the lamellae; pileus scaly, more rarely merely granulose, but smooth on the disc (« calotte ») which has a cuticle made up by a palisade of long, usually straight elements (sometimes, however, the palisade becomes appressed with repent bunches of more or less agglutinate hyphae); annulus movable, consisting of hyphae with clamp connections (at least in normal, i. e. heterothallic individuals); volva initially present but indistinct, and not persistent. On the soil in and outside the woods.

Development of the carpophores : Hemiangiocarpous.

Area : Almost cosmopolitan.

Limits : Some authors still call all the *Agaricaceae* either *Lepiota* or *Agaricus*. In this delimitation, the genus *Lepiota* would be of enormous size, and would contain the most extreme elements. In this regard, the situation is much like that in the boletes before they were revised. Heim and Romagnesi recognize both this genus (under the name *Leucocoprinus*) and *Hiatula* (i. e. *Leucocoprinus*) in addition to *Lepiota*. These authors leave *Chlorophyllum* in *Macrolepiota* (or as

they call the latter: — *Leucocoprinus*) because of the similarity of the macroscopical characters as well as most microscopical characters. However, the spore print is different in the two genera, a character which in itself unless accompanied by other correlated characters would be insufficient to separate *Chlorophyllum* on a generic basis. The author (1939) also agreed to this point of view. But, since then, the correlated characters have come to the attention of the taxonomists, viz. the absence of clamp connections, the poisonous properties, and the different behavior of the spores in a mount first stained with cresyl blue and then with phloxine whereby an intramembranal space remains pink while a strong solution of cresyl blue alone dyes the spores so deeply blue that no distinct metachromatism can be observed. This may be due to some oily contents that are perhaps also responsible for the spore color on white paper and the greenish color of the mature hymenophore All these characters of *Chlorophyllum* distinguish it from *Macrolepiota*. One may also add the predominantly tropical and subtropical distribution of *Chlorophyllum* as compared with the cosmopolitan but predominantly temperate distribution of *Macrolepiota*. *Leucogaricus* differs from *Macrolepiota* in the absence of clamps, in addition to a few minor characters, mainly those of the surface of the pileus and the size of the spores.

State of knowledge : This genus has frequently been studied by mycologists, among others by Locquin who has published several interesting facts on the whole tribus. However, the genus has never been monographed in the true sense of the word, and the determination of the species is still not easy. The most important species of the northern temperate zone are comparatively well known, especially the type species. Locquin has added a few species to those previously known but it is doubtful whether or not the reddening of the context is actually a constant character. The author has studied a very large collection of *Leucoagaricus Badhamii* from a greenhouse in Massachussetts; some of the carpophores — all equally fresh — stained strongly, others were absolutely unchanging on exposure, while still another group showed slight discoloration. As the usual chemical reactions which are ordinarily as charasteristic for this species as is the reddening of the context, have proved to be entirely parallel to the reaction induced by the oxygen of the air, the author concluded that had these specimens been collected in small number and at different locations in the open country, they may have been split

scription of new species mainly on the basis of the characters of autoxidation in *Leucocoprineae* is at least subject to skepticism, and the author does not accept this character as a basic one for the subdivision of the genera of the *Leucocoprineae.* On the other hand, there are undoubtedly many more species in existence than the four indicated below. In the steppes of the Altai Mts., a species occurs which is apparently undescribed, but is one of the leading fungus species in this kind of environment. Many described species which are preserved in various herbaria have not yet been restudied, and it is very probable that some of them will be transferred to *Macrolepiota* as soon as careful type studies show that they have clamp connections.

Practical importance: All species of *Macrolepiota* tested thus far have been found to be edible. Some are first rate mushrooms that are highly priced in the European, Asiatic and African markets, especially *M. procera.* They have not yet been grown in mushroom houses. They all fruit with great regularity at the same places year after year in spite of the fact that they are not mycorrhizal.

SPECIES

M. procera (Scop. ex Fr.) Sing. (Lepiota, Quél.; Leucocoprinus, Pat.); *M. mastoidea* (Fr.) Sing. (Lepiota, Quél.; Leucocoprinus, Sing. 1939); *M. rachodes* (Vitt.) Sing. (Lepiota, Quél.; Leucocoprinus, Pat.); *M. kerandi* (Speg.) Sing. (Lepiota, Speg.); *M. bonaerensis* (Speg.) Sing. (Agaricus, Speg.); probably also *Leucocoprinus naucinus* sensu Locquin non al. and *Agaricus (Lepiota) platensis* Speg.

KEY TO THE SPECIES

In view of the situation commented on in the paragraph on the state of knowledge, the publication of a new key to the species of this genus seems to be unadvisable. The reader is referred to the existing keys by Lange (*Flora Agaricina Danica* 1: 21. 1935), Kühner (*Bull. Soc. Myc. Fr.* 52: 195 1936), and Locquin (*Bull. Soc. Linn. Lyon*, 14: 30. 1945). These keys are intended for the European species, but many non-European species can be determined by using them.

83. LEUCOAGARICUS (Locquin) Sing.

Sydowia **2** : 35. 1948.

Type species : Leucoagaricus macrorhizus (Locquin) Sing.

Syn. : Leucocoprinus subgenus *Leucoagaricus* Locquin, *Bull Soc Linn.* **12** : 92. 1943.

Characters : Those of the tribus ; spores in print pure white, sordid cream color, or pink ; under the microscope usually small, i.e. below 10 μ in length, only in one species gigantic (*L. excoriatus*) ; with narrow and moderately distinct to broad and very distinct germ pore, with distinctly pluristratous wall which is either smooth, or ornamented with nail shaped or warty to reticulate (exosporial) excrescences, always metachromatic in cresyl blue, and not strongly deep blue everywhere as in *Chlorophyllum ;* hyphae without clamp connections, nonamyloid ; annulus fixed, finally becoming movable or remaining fixed ; surface of the pileus either scaly, or even, or fibrillose, pubescent or glabrous, sometimes with strongly excoriate margin (i. e. outer portion of the pileus strongly lacerate) ; volva none in the species studied. On the soil, on dung, on tan, on sawdust, on decayed wood, in and outside the woods.

Developement of the carpophores : Hemiangiocarpous.

Area : Almost cosmopolitan, but with an outstanding display of forms and individuals in tropical America.

Limits : This genus is intermediate between *Macrolepiota* and *Leucocoprinus.* It has the fleshier pileus and the habit of *Macrolepiota* and the clampless hyphae of *Leucocoprinus.* Some species such as *L. naucinus* and *L. excoriatus,* also *L. Badhamii,* are close to *Macrolepiota* (but clampless), whereas *L. meleagris* with its short sulcate margin was once transferred to *Leucocoprinus,* (or rather *Hiatula* in the nomenclature adopted from Heim & Romagnesi) by Singer (1936) before the group *Leucoagaricus* had been proposed by Locquin. At the same time, the larger species were usually considered as congeneric with the species of *Macrolepiota.* However, it would undoubtedly be very difficult to maintain *Macrolepiota* and *Leucocoprinus* as independent genera unless the group of species intermediate between them, viz. *Leucoagaricus,* is admitted on the same level. The separation of *Leucoagaricus* from *Macrolepiota* and *Leucocoprinus* is

also some other characters which are not usual in *Macrolepiota.* They either have excoriated rather than scaly pileus, or they have the annulus not movable, or simple and fugacius instead of movable, double and persistent, or else they have the spores much smaller than in typical *Macrolepiotae*, or the surface of the pileus is smooth and glabrous to finely pubescent or fibrillose, or they lack the volva in the primordia. Usually several, but at least one of these aberrant characters is correlated with the lack of the clamp connections. Unfortunately, the clamp connections, the most decisive character, are not always easy to observe in *Macrolepiota,* and consequently, the statement that clamp connections are present or absent, must be based on very careful and time-consuming observations. In *Leucoagaricus,* so-called false clamps are occasionally observed, and may cause misinterpretations, and, on the other hand, one will always find a few clampless septa in any tissue of the species of *Macrolepiota.* Also, the covering layers are often clampless in ortherwise clamp bearing species of *Macrolepiota.* It is therefore specified that the velar tissue must be examined; especially the cotton like inner portion of the annulus is apt to give more conclusive results than other portions of the tissue. In spite of these technical complications, the character as such is dependable and sharp — either positive or negative. It is here preferred to the characters emphasized by Locquin because *Leucoagaricus Badhamii* (considered as *Macrolepiota* by that author) and *L. meleagris* (*Leucoagaricus*, sect. *Anomalae*) are so closely related that they are even considered as identical by some authors, e. gr. Ricken, yet, in Locquin's arrangement, they are in different subgenera (or genera). In Locquin's *Naucini* one can find all characters known in *Leucoagaricus,* and Locquin mentions their « transitional » position. In the author's opinion, they belong in *Leucoagaricus,* as emended here, excepting probably the *Macrolepiota* called *Leucocoprinus naucinus* by Locquin, but this species is not what the majority of the authors, including Fries, used to call *Lepiota naucina,* at least judging from the specimens and descriptions available.

The separation of *Leucoagaricus* from *Leucocoprinus* is somewhat more complicated.

In fact, some species of *Leucoagaricus,* e. gr. *L. meleagris,* have sulcate margins as has been mentioned above, and this fact makes the differentiation on this basis quantitative rather than qualitative with several possibilities as to where to put the delimiting line. However, it appears that it would not be correct to separate the species with

reddening context or those staining yellow, from the other *Leucoagarici* characterized by such phenomena of autoxidation, and consequently, the line between *Leucoagaricus* and *Leucocoprinus* should be drawn so as to leave *L. meleagris* in the same genus as *L. Badhamii*. *Leucocoprinus* is therefore defined as having a sulcate pileus not merely in the external zone of the margin but all over a substantial part of the surface of the pileus, and the pileus must be membranaceous everywhere instead of fleshy in the center.

Buller's investigations on the hymenia of the agarics may eventually turn out to offer the best way of distinction between *Leucoagaricus* and *Leucocoprinus*. He states that the large species of the group *M. procerus* have hymenia of the *Panaeolus* subtype, i. e. a subtype of the aequihymeniiferous type where the basidia are monomorphous, the pseudoparaphyses not well developed, and the spores maturing in areas alternating with other areas where the basidia are not yet sporulating. In dark spored agarics, this arrangement causes a marbled appearance which also appears in the hymenium if first treated with iodine, preferably by Gilbert's [101] method, or, if very thin sections are made slicing off the hymenium of one side of the lamella, by using Melzer's reagent on the white-spored agarics with amyloid or pseudo amyloid spores. This same result was obtained by the author when fresh material of *Leucoagaricus excoriatus* and *L. rubrotinctus* were checked. In *Leucocoprinus* however, Buller indicated the occurrence of the *Psathyrella* subtype (*Leucocoprinus cepaestipes*). The author found tri- to tetramorphous basidia and a short sporulating period in some of the tropical yellow *Leucocoprini* in Florida. It may be assumed that all *Leucoagarici* belong to the *Panaeolus* subtype, and all *Leucocoprini* to the *Psathyrella*-subtype. However, it would be preferable to check on this character further by examining the hymenophoral structure of all *Leucoagarici* and all *Leucocoprini* before this character is emphasized as the main microscopical distinction between the two genera.

The genus *Chlorophyllum* can be distinguished from *Leucoagaricus* by its external characters which are all more like those of *Macrolepiota* excepting the green spore print which, however, may also be ochraceous at times; microscopically, the behavior of the spores in cresyl blue and their large size which is comparable only to the size

[101] Gilbert, E. J., *Emploi des vapeurs d'iode en mycologie. Bull. Soc. Myc. Fr.* **45**: 141-144, 1929.

of the spores of *Leucoagaricus excoriatus* (but the latter has white spore print), distinguish *Clorophyllum* from *Leucoagaricus.*

Though it may appear to be difficult for those who are used to simpler methods, to distinguish the genus *Leucoagaricus* on the basis of the absence of clamp connections and the presence of the metachromatism in the spores, the author's experience points at a possibility of recognizing the genus *Leucoagaricus* right in the field. The habit of the carpophores is characteristic because of the shorter stipe which — as the name seems to suggest — tends to make these fungi appear like light-spored *Agarici.*

State of knowledge : Most species entering this genus were either little known or not known at all, even a very few years ago. Since then, the author has studied the types of several so called *Lepiotae*, and many of these were found to be congeneric with the type species of *Leocoagaricus,* a European species studied by the author at the same time and compared with the additional species transferred here to this genus. Though it cannot be claimed that the majority of species that will go to *Leucoagaricus* in the end, are known at present, our knowledge is satisfatory now in the sense that it is apt to provide a general understanding of the outlines of this genus. On the basis of the type studies carried out thus far, nine species are now admitted in the genus *Leucoagaricus,* and according to the investigations and descriptions by other authors about an equal number can be added with confidence. The chemical characters as well as more detailed anatocomical data, and also further type studies especially in the American tropics will reveal many more species which will be transferred to *Leucoagaricus* before long.

Practical importance : This genus, in contrast to *Macrolepiota,* does not contain important edible mushrooms, but, on the contrary, many of the species have repeatedly and perhaps justly been suspected to cause ill effects when used as food. Locquin has recently confirmed that the true *L. Badhamii* is inoffensive, even edible, yet, other species will still be suspected as long as they are not all tested after exact identification. It seems that some of the African species are actually poisonous.

SPECIES

Sect. 1. **MACROSPORI** Sing. (1948) Spores 12-16 μ large; pileus not bright colored; context and spores not darkening; annulus eventually becoming movable.

L. excoriatus (Schaeff. ex Fr.) Sing. (Lepiota, Quél.; Leucocoprinus, Pat.).

Sect. 2. ANOMALI Locquin (1945). Spores medium sized; pileus scaly; context reddening or staining yellow, or both; spore print usually white; annulus eventually becoming movable.

Type species: L. meleagris (Sow. ex Fr.) Sing.

Aside from the type especies, some other species closely related to it, enter this section. However, the author prefers to refrain from naming them since their status as well as their nomenclature do not appear to be finally settled.

Sect. 3 TYPICI Locquin (1945). Not combining the characters of sect. 1, or those of sect. 2, and pileus not bright colored as in sect. 4.

Type species: L. macrorhizus (Locquin) Sing.

L. macrorhizus (Locquin) Sing. (Leucocoprinus, Locquin); *L. sublittoralis* (Kühner) Sing. (Lepiota, Kühner); also *L. ianthinofuscus* (Locquin) according to Locquin.

Sec. 4. RUBROTINCTI Sing. (1948) Pileus bright colored at least on the disc and scales; endosporium of the spores sometimes indistinct and very faint in cresyl blue, perisporium often very strongly developed and in two species forming a distinct persistent ornamentation; context unchanging; spore print usually white. Mostly American and tropical species.

Type species: L. rubrotinctus (Peck) Sing.

L. rubrotinctus (Peck) Sing (Lepiota, Peck); *L. rubrosquamosus* (Rick) Sing. (Lepiota, Rick); *L. olivaceus* (Kauffman) Sing. (Lepiota, Kauffman); *L. olivaceomamillatus* (Rick) Sing. (Lepiota, Rick); *L. confusus* (Rick) Sing. (Lepiota, Rick).

KEY TO THE SPECIES

A. Spores gigantic: 12-16 μ long. *L. excoriatus*

A. Spores smaller.

B Pileus scaly, at least in the outer part of the pileus.

C At least a majority of the specimens of a population stain yellow or red or both when touched or bruised; scales and disc rarely not brown. *L. meleagris* and allied species

C Context unchanging or almost; color of the scales and disc of the pileus usually red, pink, orange, or olive color.

D Spores with a reticulation formed by a layer of the spore wall which is deep violet in cresyl blue; epicutis hymeniform, its elements balloon-shaped. *L. rubrosquamosus*

D. Spores smooth, and if there is a distinct outer layer it is close-

ly attached to the episporium and can be seen only in cresyl blue where it is deep violet.

F Lamellae white: North America

L. olivaceus, and olive forms of *L. rubrotinctus*

F' Lamellae yellowish orange South American species (probably also some African species keying out here

L. olivaceomamillatus and *L. confusus*

B Pileus naked and glabrous, or sericeous, or pulverulent, or floccillose

E A majority of the specimens in a population turning yellow or brown; spores often pinkish in print

L. naucinus and allied species

E. Context unchanging

G Pileus brownish silky-fibrillose, stipe with pseudorhiza.

L. macrorhizus

G. Pileus at least in the beginning white or whitish.

H. Annulus eventually becoming movable

(see *L. naucinus* aff.)

H' Annulus remaining fixed to the stipe, infund bulbiform

L. sublittoralis

84. LEUCOCOPRINUS Pat.

Bull. Soc. Myc. Fr. **4**: 26. 1888

Type species: L. flavipes Pat.

Syn. *Mastocephalus* Batt. ex O. Kuntze, *Rev. Gen. Pl.* **2**. 857. 1891.
? *Hiatula* (Fr.) Mont., *Ann. Sc. Nat.* IV. **1**: 107. 1854 (vix sensu originali);
Hiatula sensu Heim & Rom. (1934); Singer (1936)
? *Leptomyces* Mont., *Syll. Cryptog.*, p. 128. 1856

Characters. Those of the tribus; habit of the carpophores much like that of the thinner *Coprini*, a substantial portion of the pileus, at least the marginal half radially split and sulcate pectinate, with very thin context even in the inner half; epicutis of the pileus formed by a mixture of different types of cells and hyphae, not by a homogeneous palisade, also not by a hymenium; lamellae thin and soft, sometimes subdeliquescent; spore print pure white to yellowish; spores with more or less distinct germ pore, endosporium always metachromatically colored when dyed with cresyl blue, non ornamented, without suprahilar applanation or depression, or with an indistinct applanation; cystidia either absent, or not numerous on the sides of the lamellae; cheilocystidia usually numerous; clamp connections usually absent; tissue nonamyloid; hymenophoral trama more or less regular; stipe usually with an annulus which is usually

movable at least in age: cup shaped volva none. On the earth or on various hosts.

Development of the carpophores: Probably always hemiangiocarpous.

Area: Warmer part of the American continent, common in the tropics of both hemispheres, also often found spontaneously growing in greenhouses.

Limits: As for the delimitation of this genus from *Leucoagaricus*, see there. The other genera of the *Leucocoprinaceae* are clearly separated by the characters indicated in the key. The rare cases where some clamp connections have been observed in *Leucocoprinus* should not cause any difficulties because the only other genus with clamp connections, *Macrolepiota*, is vastly different in the habit of the carpophores. Besides, the author has never found any clamps in any species, except one, later (1943) reported as *Hiatula lutea*. This is probably exceptional.

State of knowledge: This genus has never been studied monographically. Some authors have treated it as an appendix to essays on *Lepiota* — yet most of the species macroscopically similar to *Leucocoprinus* or *Hiatula*, have never been subjected to serious type studies until a number of them were taken up by the author in preparation for the present work. Nine species have been admitted.

Practical importance: At least one of the yellow species is violently poisonous.

SPECIES

L. luteus (Sow. ex Secr.) Locquin [Hiatula, Sing. 1943; Lepiota, Godfrin; Agaricus cepaestipes luteus Secr.; Lepiota flammula (A. & S. ex aut.) Gillet; Agaricus flos-sulphuris Schnizlein]; *P. cepaestipes* (Sow. ex Fr.) Pat. sensu str. (Lepiota, Quél.; Hiatula, Heim & Romagnesi); *L. lilacinogranulosus* (Henn.) Locquin (Lepiota, Henn.; Hiatula cepaestipes var. lilacinogranulosa Heim & Romagnesi); *L. Magnusianus* (Henn. apud Rab.) Sing. (Hiatula Sing. 1943; Lepiota, Henn. apud Rab.); *L. Brebissonnii* (Godey) Locquin (Lepiota, Godey; Hiatula, Sing. 1943); *L. fragilissimus* (Berk. & Rav.) Pat. (Lepiota licmophora Berk. & Br.); *L. denudatus* (Rab.) Sing. (Agaricus, Rab.; Lepiota, Sacc.; Lepiota Gueguenii Sacc. & Trav.; Lepiota Boudieri Guéguen non Bres.); *L. melanoloma* (Sing.) Sing. (Hiatula, Sing.);

KEY TO THE SPECIES

The species indicated above are all specifically different from each other, and a comparison with the original material and diagnoses will lead to reliable identifications. However, considering the large number of species not yet studied, the author cannot publish a key at the present time.

GENERA INCOMPLETELY KNOWN

Hiatula (Fr.) Mont., *Ann. Sc. Nat.* IV. 1: 107. 1854. « Pileus very thin, without cuticle, formed by the interlamellar hypophyllous tissue (e dorsis lamellarum junctis formatus) as in the thinnest *Coprini*, but not deliquescent, and spores white. » Fries, *Nov. Symb.*, p. 27, *Hiatula*, subgenus *Agarici* (1851). The type species is *Agaricus (Hiatula) Benzonii* Fr. This as well as the other species cited by Fries is too incompletely known to be interpreted with certainty. Fries has not left any specimens at Upsala, and the published drawings were made later from material that he received from greenhouses in Europe, and believed to be the same species (which is very doubtful); other material was later determined by Fries but the only authentic specimens in existence are those sent to Fries by Oudemans, and these are according to Oort (*Meded. Ned. Myc. Ver.* 16-17: 249. 1928, close to *Pseudocoprinus cepaestipes*, but do not correspond to the description, and the illustrations by Fries and Gonnermann & Rabenhorst since they have a scaly pileus and an annulus. Consequently, there must have been additional material seen and determined by Fries which cannot be located at present, and which has probably been lost. Under these circumstance, the author does not think it possible to maintain the genus *Hiatula* in the sense of Heim and Romagnesi (also the sense of Singer 1936, 1943). Since in spite of Dr. Nannfeldt's cooperation nothing more conclusive could be found out about the type of *Hiatula*, *Hiatula* in the sense of Heim & Romagnesi — unless conserved — will not stand up against the genus *Leucocoprinus* as here admitted in preference to *Hiatula*. *Hiatula* is a genus without much practical importance, and the number of combinations made in that genus is not large. It can be foreseen that the conservation of *Hiatula* in the sense of Heim & Romagnesi (= *Leucocoprinus*) would hardly find a majority in a Botanical Congress; on the other hand, the problem is complicated by the existence of the genus *Leptomyces* Mont. It is quite possible that mate-

rial of the latter will be found at Paris, and if determinable, it might upset any arrangement made in regard to *Hiatula.*

It is worth mentioning that the only material of *Hiatula Benzonii* ever distributed is that published by Rick. This material is sterile. It is evidently a sterile form of some *Coprinus.* It seems to the author that this is also the most probable solution of the whole problem. Fries has probably not seen a spore print of any of these *Hiatulae,* perhaps not even dried specimens but merely drawings. In spite of the fact that he says « sporidia alba », all he noticed was the whitish color of the lamellae. This whitish color can very well be explained by sterility of the *Coprini* that were the subject of Fries' early publications on *Hiatula.* Later on, he probably confused them with various agarics, among others the genus *Leucocoprinus.*

Hiatula should be entered in the list of genera dubia — unless, quite unexpectedly, type material can be uncovered somewhere in Europe (perhaps in Denmark ? — Benzon was a Dane).

Leptomyces Mont., *Syll. Gen. Spec. Crypt.*, p. 128. 1856. « Carpophore very thin-membranous, transparent; lamellae very thin, close, free; trama none; stipe fistulose, glabrous, smooth, separable from the pileus; spores white, transparent, very numerous, stuffed with a nucleus (oil drop ?); wood-inhabiting fungi ». Montagne. The type species is *L. lignifragus* (Mont.) Mont. from French Guyana (Leprieur, n° 985). Unless this material is reexamined, no positive conclusions can be made. It has been suspected — by Montagne as well as by others — that *Leptomyces* is the same as *Hiatula.* If *Hiatula* is a sterile form of a *Coprinus* sp. then, *Leptomyces* is definitely different from it since Montagne has seen « very numerous » spores and described them. However, the description of the striation of the pileus is not suggestive of *Leucocoprinus,* and unless the type specimen — if preserved — shows that the description is not adequate, *Leptomyces* cannot replace *Leucocoprinus.* This is one of the cases in generic taxonomy where further type studies may clear up an obscure situation, or else prove that *Leptomyces,* and *Hiatula,* are permanently dubious genera.

Lepiotella Rick, *Lilloa* 2: 251. 1938, non (Gilbert) Gilbert ex Kühner & Maire (1934). « Stipe with differentiated volva and persistent annulus; lamellae remote; consistency not fleshy but cottony-soft. » Rick. The type is *L. brunnea* Rick from Brazil with radially fibrous and squarrulose, umbonate, large pileus, and narrow, white lamellae; the stipe is squarrose and marbled, the annulus brown and movable;

the spores were not observed. From this description there seems to be little doubt but that it refers to the *Leucocoprineae*; on the other hand, it is impossible to tell whether or not it deserves generic rank. It is probable that the type is a young carpophore with the volva still intact, and the spores not yet formed. It may then be an extreme form of *Clarkeinda, Macrolepiota*, or *Leucoagaricus*. Under these circumstances, it would be unwise to create a nomen novum for this genus which is a homonym by four years, if Gilbert's claim in Kuhner & Maire is recognized as a new status of Gilbert's subgenus of 1918; otherwise by two years, since Gilbert's claim was accepted by Singer (1936).

Schinzinia Fayod, *Verh. Bot. Ver. Brandenburg* 31: 227. 1890. « Characters of *Pluteus* but with tough consistency ». Fayod. The type species is *S. pustulosa* Fayod from East Africa. The abbreviated description above does not give an impression of the affinities of this species. The good figures published by Fayod (*l. c.* pl. 3) leave no doubt but that this is a genus of the *Leucocoprineae* since the thick walled spores have a germ pore. However, there is no indication on the clamp connections, and besides the metachromatism of the spore wall in cresyl blue is not known. Even so, the genus *Schinzinia* might be recognized as valid were it not for the fact that the material comes from an exotic region where it had been collected by a non-mycologist. The movable annulus of the *Leucocoprineae* tends to fall off dried specimens, and it is almost probable that *Schinzinia* is just such a mutilated *Macrolepiota* or more probably *Leucoagaricus*. Africa is very rich in species of *Leucocoprineae*, some of them with pink spores. Unless more good material from the type locality is examined, it is felt that *Schinzinia* should not be admitted on the same level as *Macrolepiota* and *Leucoagaricus*.

Tribus AGARICEAE Pat.

Hym. Eur. p. 75. 1887 (ut Agaricés); Henn. in Engl. & Pr., *Nat. Pfl.* I. 1**. 230. 1898. sensu str. Konr. & Maubl., *Ic. Sel. Fung.* **6**: 57. 1924.

Type genus: Agaricus L. ex Fr. sensu stricto Karst.

Syn.: *Psallioteae* Fay., *Ann. Sc. Nat., Bot.* VII **9**: 352. 1889 (ut Psalliotés); R. Maire, *Publ. Inst. Cienc. Nat. Barcelona* **1933**: 83. 1933.
Psalliotoideae (subfam. *Coprinacearum*) Sing. *Ann. Mycol.* **34**: 340. 1936.

Characters: Spores with complex walls which are neither distinctly pseudoamyloid, nor amyloid; with or without germ pore,

always strongly colored when dehydrated (often changing from green to brownish purple) or brownish purple to sepia in fresh condition, the walls sometimes heterogeneous and appearing punctate; always more or less colored under the microscope, and never white, cream color, or pale pink in print; volva sometimes well developed and cup shaped-saccate, or else forming an annular volva near the marginal veil or attached to it, or else volva too thin to be persistent and showing in adult specimens.

Note: This tribus corresponds to the genus *Psalliota* of the older authors.

KEY TO THE GENERA

A. Pileus without a cellular epicutis; spores neither punctulate nor subangular to nodose; hyphae usually without clamp connections; spore print never green to olive.

B. Cheilocystidia none, or vesiculose, spores usually not visibly pseudoamyloid; print not « burnt umber » (Maerz & Paul) 85. *Agaricus*

B. Cheilocystidia elongate, conspicuous; spores pseudoamyloid; print « burnt umber ». (see *Lepiota*, p. 439, 441)

A. Pileus with a distinct epithelium; spores either punctulate or subangular to nodose (as in *Inocybe*); hyphae usually with clamp connections; spore print sometimes green to olive.

C. Spore print initially green to olive, becoming purple or brownish purple by dehydration; spores punctulate rather pale colored under the microscope, not subangular to nodose. 87. *Melanophyllum*

C. Spore print never green to olive; spores perfectly smooth but subangular or nodose in outline, deep colored under the microscope. 86. *Cystoagaricus*

85. AGARICUS L. ex Fr.

Syst. Mycol. 1: 5. 1821, em. Karst. *Bidr. Finl. Nat. Folk* 32: xxv. 1879.

Type species: Agaricus campestris L. ex Fr.

Syn.: *Pratella* (Pers. ex) S. F. Gray, *Nat. Arr. Brit. Pl.* 1: 626. 1821.
Psalliota (Fr.) Quél., *Champ. Jura Vosg.*, p. 139. 1872-73.

Characters: Habit of carpophores pluteoid, reminiscent of *Leucoagaricus*; pileus naked or squamose, also with pyramidal or areolate warts, or smooth, dry, white or colored; epicutis not cellular; most frequently consisting of appressed, elongate hyphae, or of fragments of a palisade; hymenophore lamellate; lamellae free but not with a collarium, eventually deep colored because of the attached spores; spore print purplish brown to « sepia » (Séguy): spores brown under

the microscope, smooth, with compound wall which is not visibly pseudoamyloid, with distinct or rather indistinct germ pore, more often rather small than large (i. e. rarely larger than 10 μ); basidia normal in all regards, but often consistently 2 spored, rather small; cystidia none excepting the cheilocystidia which are moderately numerous in some species, and then appear vesiculose or otherwise broad, often septate below and pedicellate, becoming obsolete in mature dried material in many cases; hymenophoral trama regular then irregular; stipe without a cellular covering, usually with a thin-membranous fugacious to thick, almost fleshy annulus and sometimes doubly annulate, and the lower annulus representing a volva which is appressed and not cup shaped near the base; context non amyloid, often changing to reddish when bruised or changing to yellow when touched; hyphae usually without clamp connections, rarely with clamp connections. On the soil and on dung, on tan, humus, anthills[103], in and outside the woods. Surfaces and context of the carpophores often strongly reacting with the ordinary reagents and with a combination (« cross reaction ») of anilin and nitric acid.

Development of the carpophores: Hemiangiocarpous, according to Atkinson and Levine.

Area: Almost cosmopolitan.

Limits: The spore color and the lack of spherocysts in the cortical layers define this genus fully. The genus *Micropsalliota* Hoehnel which was often thought to be like *Agaricus*, only smaller, has much paler, and distinctly pseudoamyloid spores, and can therefore not be considered as belonging to the *Agariceae*. The genus *Pilosace* is doubtful (see p. 436).

State of knowledge: As easy as it ordinarily is to recognize a species as belonging to *Agaricus*, as difficult is the subdivision of the genus, and the determination of the species. The enormous variety of species as seen in one of the regions richest in *Agarici*, e. gr. the North American prairies, the South American pampas, the Central Asiatic steppes, and the lawns and open places in Florida, make it very difficult to assemble enough knowledge on each of the species to insert it correctly in any natural classification or key. The main difficulty is that any natural subdivision of the genus *Agaricus*

[103] Judging from the original account which includes a photograph, the often cited *Rozites gongylophora* Moeller is not a *Rozites* but an *Agaricus* sp. The same is probably true for another agaric inhabiting anthills, viz *Locellina Mazzuchii* Speg. (*Rev. Mus. La Plata* 26 : 166. 1921).

must at least partly rely on characters that are visible only in fresh material, i. e. chemical reactions of the fresh carpophores, and changes in color caused by bruising or touching of the fresh carpophores. Even if all the characters of all the species were known, it would still be difficult to subdivide *Agaricus* because the chemical reactions are not fully constant, though much more so than the color changes caused by autoxidation.

Nevertheless, the author believes that the most natural classification is one based on the data supplied by Schaffer & Moeller (*Ann. Mycol.* 36 : 64. 1938). The exact spore measurements for most of the type specimens of American *Agarici* by A. H. Smith will also be a valuable help for future monographic studies. It must be hoped that future work will reveal additional reliable characters because the characters now considered as decisive are all either difficult to state, or inconstant, or merely too few. At present, only 20 species are admitted.

Practical importance. This state of taxonomic knowledge of the genus *Agaricus* is regrettable inasmuch as the genus is of economic importance. Only two species are supposed to be slightly poisonous at times (*A. silvicola*, *A. xanthoderma*); all others are edible, and range from excellent to fair in food value. Some have been grown commercially, e. gr. *A. bisporus* (most widely used by commercial growers), *A. bitorquis*, *A. arvensis*, and others. The most important edible mushroom in the temperate regions of Europe and North America is undoubtedly *A. bisporus*. The production of carpophores for the food market has become a major industry, at first in France, and later in other countries. Now, according to the volume of production, the United States ranks first. Other mushroom growing countries are Hungary, Austria, Germany, The Netherlands, Canada, Argentina, Australia, and the U. S. S. R. In tropical countries, this species is replaced by species whose culture is cheaper because they do not need refrigeration (as *A. bisporus* does). Strangely enough, the species replacing *A. bisporus* in the tropics are not other, tropical species of the same genus but rather *Volvariella*. The « white mushroom » is imported to the tropics in cans.

During the last few years it has become possible to utilize, by the application of new methods, all kinds of refuse material left over from the mushroom production for the food market, and to extract vital industrial products others than food. It remains to be seen whether these processes will hold their place in peace time.

Aside from the cultivated species, many other species are often collected by the inhabitants of various regions. Wild *Agarici* are especially in demand in Europe, all parts of Asia, especially Transcaucasia, Siberia, Indo China, China, India, Java, Japan, and the Philippines.

SPECIES

Sect. 1. **CAMPESTRES** Konr. & Maubl. (1924) em. (*Rufescentes* Schäff. & Moell. 1938). Context of the pileus reddening on bruising or staining brick orange, or unchanging in wounds but becoming slightly reddish in age; spores globose or ovoid-ellipsoid, always globose or nearly so in the species with reddening context; anilin oil reacting deep reddish brown on the surface of the pileus, or negative. Species growing in open places outside the woods.

Type species : A. campestris L. ex Fr.

A. campestris L. ex Fr.; *A. bisporus* (Lange) Sing. [100] [Psalliota, Schäffer & Moeller; Psalliota hortensis (Cooke) W. G. Smith var. bispora Lange; Agaricus hortensis (Cooke) Konr. & Maubl. non Fr.]; *A. subperonatus* (Lange) Sing. [Psalliota hortensis var. subperonata Lange; Psalliota subperonata (Lange); Lang.; A vaporarius (Pers. ex Vitt.) Schäffer & Moeller non Otto ex Krombholz; A. campestris B. pratensis α vaporarius Vitt.; Psalliota bivelata Velen. non Agaricus bivelatus Peck]; *A. Bernardii* (Quel.) Sacc.; *Agaricus bitorquis* (Quél.) Sacc. [Psalliota, Quél.; Agaricus Rodmanii Peck; A. campestris var. edulis Vitt.; Psalliota campestris var. edulis Bres.; Agaricus peronatus Rich. & Roze; Chitonia Pequinii Boudier; Clarkeinda, Bres.; Agaricus, Konr. & Maubl.; Psalliota edulis (Vitt.) Schaffer & Moeller; Chitonia, Herrfurth]. Probably also here: *A. solidipes* Peck, and *A. urinascens* (Schäffer & Moeller) Sing. (Psalliota, Schaffer & Moeller).

[100] One can find in all popular articles and botanical text books the erroneous indication that the scientific name of the cultivated white mushroom is *A. campestris*, or *Psaliota campestris*. Some add that the 4-spored basidia of the wild white mushroom become 2-spored when the fungus is grown in mushroom houses, or cellars. In a careful comparative study of the macroscopical, chemical and anatomical characters of *A. campestris* and *A. bisporus*, the author has found these species to be very different, and a 4-spored *A. bisporus* would be near *A. subperonatus* rather than near *A. campestris*. It is doubtful whether the true *A. campestris* has ever been grown commercially, and it may be expected that these facts will at last be acknowledged by botanical writers.

Sect. 2. **SANGUINOLENTI** Schäffer & Moeller (ut sect. *Psalliotae*, 1938). Characters of section 1 but growing in the woods rather than in open places, and combining a slight reaction with anilin oil on the context with a strong reaction (slowly dark brown) with the same reagent on the surface of the pileus.

Type species : A. silvaticus Schaeff. ex Secr. sensu Krombholz

A. silvaticus Schaeff. ex Secr. sensu Krombholz [Psalliota, Quél. ; Psalliota sanguinaria (Karst.?) Lange sensu Lange]; *A. haemorrhoidarius* Schulz. (sensu Lange ; *A. lanipes* (Moeller & Schaffer) Sing (Psalliota, Moeller & Schaeffer); probably also *A. Benesii* Pilát.

Sect. 3. **ARVENSES** Konr. & Maubl. (1924) (*Flavescentes* Schaffer & Moeller). Carpophores tending to become yellowish on pressure but sometimes unchanging; surfaces yellow or orange with NaOH or KOH ; orange red or fire red with « cross reaction » (i. e. one streak of anilin oil over the surface of the pileus crossed with another streak of concentrated nitric acid ; the discoloration appears where the two reagents mix).

Type species : A. arvensis Schaeff. ex Fr.

A. arvensis Schaeff. ex Fr. (Psalliota, Quél. ; A. edulis Krombh. non Psalliota edulis Schaffer & Moeller ; Pratella edulis S. F. Gray); *A. stramineus* (Schaffer & Moeller) Sing (Psalliota, Schaffer & Moeller; Psalliota lepiotoides Roman Schultz non al.?) ; *A. silvicola* (Vitt.) Sacc. (Pratella flavescens Gillet ; A. campestris var. silvicola Vitt.); *A. abruptibulbus* Peck; *A. augustus* Fr. (Psalliota, Quel.), and, if different from the latter, two very closely related species: *A. perrarus* Schulzer and *A. elvensis* Berk. & Br.; *A. projectellus* Murr.; *A. cylindriceps* Murr.; *A. pocillator* Murr.; *A. bambusigenus* Berk. & Curt ; probably also *A. semotus* Fr., *A. exquisitus* Vitt., and *Psalliota duriuscula* Rea.

Sect. 4. **XANTHODERMATEI** Sing. (1948) Characters of the preceding section but the reaction with anilin oil on the pileus and context bright and deep yellow to orange and the « cross reaction » negative.

A. xanthoderma Genevier (Psalliota, Richon & Roze ; Agaricus coloformicus Speg ; Psalliota meleagris J. Schaffer) and its varieties, e. gr. var. *lepiotoides* Maire, var. *obscuratus* Maire, var. *ammophilus* (Ménier) Maire.

Note *Stropharia crocopepla* (Berk. & Br.) Sacc. and many species indicated by Saccardo as *Agaricus* belong undoubtedly in *Agaricus* but they cannot be inserted in the correct section.

KEY TO THE SPECIES

It is impossible to give a workable key to the species of *Agaricus* at the present moment.

86. CYSTOAGARICUS Sing

Mycologia, 39 : 85. 1947.

Type species : *Cystoagaricus Strobilomyces* (Murr.) Sing.

Characters : Habit of the carpophores pluteoid, much like that of the small species of *Agaricus*, or one of the shaggy species of *Agaricus*, or else collybioid; pigment in the tissues of the cortical layers usually incrusting the hyphal walls, dark or very bright, pileus strongly convex or applanate, mealy, or furfuraceous, or squarrose spinose; uppermost layer of the pileus (velar ?) consisting of a dense mass or loosely arranged chains of subisodiametrical cells, in other words — an epithelium; lamellae free to very narrowly adnexed, ascendant or subhorizontal, moderately broad to rather broad; spore print brownish fuscous with a purplish tinge. under the microscope dark brownish fuscous or purplish fuscous, in KOH medium sometimes becoming olive brown, small but sometimes reaching about 10 µ, with double wall which does not change color in Melzer's reagent, with somewhat indistinct to very broad and distinct germ pore, often even truncate, the hilum not projecting but strongly eccentric, without suprahilar applanation or depression, with curved-nodose or subangular outline at least in a majority of mature spores, somewhat elongate to subisodiametric; basidia normal, small, four-spored ; cystidia on the sides of the lamellae none ; cheilocystidia pluricellular consisting of short chains of vesiculose elements which make the edge of the lamellae heteromorphous; hymenophoral trama regular, later subregular, consisting of voluminous elongate elements ; subhymenium subcellular ; stipe central, squarrulose or furfuraceous like the pileus, sometimes with annular veil, the furfuraceous or squarrulose particles also consisting of sphaerocysts ; context thin, more rarely medium thick ; hyphae non amyloid, with clamp connections. On wood, and on moist sand ; solitary, gregarious, or subfasciculate.

Development of the carpophores : Unknown.

Area : Florida, Liberia, and Zanzibar: most probably pantropical.

Limits : Micropsaliota Hoehnel which may be suspected to be congeneric, is actually a synonym of *Lepiota* as shown by the original

specimens preserved at the Hoehnel Herbarium. The spores of these Javanese specimens are paler with a more consistently even outline and a distinct pseudoamyloid reaction. The structure of the upper layer of the carpophores is suggestive of *Psathyrella* in both species of *Cystoagaricus*, but in *Psathyrella* the lamellae are usually more broadly adnexed or adnate, and a combination of pseudoparenchymatic veil and septate cheilocystidia of the vesiculose type is never observed; in certain forms considered, at present, as species of *Psathyrella*, the spores may appear subangular but their outline is different from that observed in *Cystoagaricus*. In the writer's opinion, *Cystoagaricus* and *Psathyrella* are related only insofar as the families to which they belong (*Agaricaceae* and *Coprinaceae*) are related with each other.

State of knowledge : Two species are known at present; more will probably be discovered in the future.

Practical importance : None.

SPECIES

C. Strobilomyces (Murr.) Sing. (Nolanea, Murr.); *C. trisulphuratus* (Berk.) Sing. (Agaricus, Berk.).

87. MELANOPHYLLUM Vel.

České Houby, **3** : 569. 1921

Type species : M. Canali Vel.

Syn : Chlorospora Mass. *Kew Bull.* for **1898**, p. 136. 1898, non Spegazzini (1891).
Chlorosperma Murr., *Mycologia* **14** : 96. 1922
Glaucospora Rea, *Brit. Bas.*, p. 62. 1922

Characters : Habit of the carpophores pluteoid, reminiscent of certain Lepiotas; pileus and stipe covered with an epithelium (from the veil); lamellae free, brightly colored; spore print blue green, or olive to green (J 2 of Lange's chart), later often becoming fuscous purple by dehydration; spores under the microscope (if taken from dried material) subhyaline to rather pale umber sepia but pigment very diluted, more concentrated only in short cylinders perforating the episporium and making the spores appear finely punctulate when the

when seen from the hilar end (the longitudinal axis of the spore pointing toward the objective) as in *Clitopilus ;* without suprahilar depression (sometimes applanate), without a germ pore, hyaline when seen floating singly in water, oblong-ellipsoid to ellipsoid, rarely a central or almost central constriction in abnormal spores and then often somewhat angular but not with a subangular or wavy nodose outline as in *Cystoagaricus ;* cystidia none on the sides of lamellae; hymenophoral trama regular; stipe central, subannulate, at least the lower portion furfuraceous to shaggy from the powdery epithelium consisting of the same spherocysts as those on the pileus and filled likewise with fuscous, dissolved pigment; context fleshy, nonamyloid, with odor of cucumbers; hyphae with clamp connections. On various substrata, mostly on the earth or on rotten tan, often in greenhouses, on manure piles, etc.

Development of the carpophores : Unknown, probably hemiangiocarpous.

Area : Europe, North and South America.

Limits : This differs from *Lepiota* with which it has been identified by Kühner and other modern authors, in having punctulate, non-pseudoamyloid spores with a very characteristic range or sequence of spore print colors. It differs from *Cystoderma* with which it had been identified by Fayod and Singer (but was removed by Smith & Singer 1945) in the free lamellae, the color of the spore print, the punctulate spores and the color of the lamellae. It differs from *Agaricus* with which it had been identified by Singer (1922) but not by other modern authors, in the initial olive green color of the spore print, the deep and rich color of the lamellae, the punctulate spores, the always clamped septa, the covering epithelia, etc. It differs from *Inocybe* with which it has been identified by some authors, in the free lamellae, the punctulate spores, the epithelium on the pileus and the stipe, and the color sequence of the spore print, also in the mealy-scaly character of the surfaces and in the small size of the spores.

State of knowledge : Only two species are completely known as far as the characters essential for their generic position are concerned. But these are at present the only species which can be inserted in *Melanophyllum* with confidence. If other species should later enter this genus, it is quite possible that the transfer may cause an emendation of the generic diagnosis.

Practical importance : The type species has been suspected to be poisonous, but some authors go so far as to call it edible.

SPECIES

M. echinatum (Roth ex Fr.) Sing. (Lepiota, Quél.; Psalliota, Quél.; Inocybe, Sacc.; Cystoderma, Sing. 1936; Agaricus fumosopurpureus Lasch; Agaricus haematophyllus Berk.; M. Canali Velen.; Agaricus olivaesporus Ell. & Ev.; Chlorosperma, Murr.); *M. Eyrei* (Mass.) Sing. (Chlorospora, Mass.; Schulzeria, Mass.; Cystoderma, Favod ex Sing.; Glaucospora, Rea; Lepiota, Kuhner).

GENERA INCOMPLETELY KNOWN

Pilosace (Fr.) Quél., *Champ. Jura Vosg.* **2**: 360. 1873 (*Agaricus* subgen. *Pilosace* Fr. *Nov. Symbol.*, p. 25. 1851.) « Pileus distinct from the stipe (Hymenophorum a stipite discretum); lamellae free and in the first species [*A. tricholepis* Fr.] remote from the stipe as in *A. procerus* [*Macrolepiota procera*]; spores fuscous; veil none; nearest to the *Psalliotae* [*Agaricus* sensu Karst.] but without any veil... » Fries. The type species is either *A. tricholepis* or *A. hololepis* Fr. The author would prefer the latter as a lectotype. Both species are based not on specimens but on figures of very doubtful value. Quélet has added a new element in describing another species in this genus, *P. algeriensis*. What this actually is, cannot be said with certainty, and even the French mycologists have only hypotheses on this subject. But even if the position of this species could be cleared up, the status of Quélet's species would have no influence on the status of the genus *Pilosace* as such. Some of these species might be exannulate *Agarici*, and this is the reason why *Pilosace* is mentioned here.

Tribus LEPIOTEAE Fayod

Prodrome, Ann. Sc. Nat., Bot. VII, **9**: 349. 1889 (ut Lepiotés); R. Maire, Publ. *Junta Cienc. Nat. Barcelona*, **1933**, p. 81. 1933

Type genus: *Lepiota* (Pers. ex) Gray.

Characters: Habit of the carpophores, hymenophoral trama, and most other characters as in the family; spores always more or less (sometimes rather weakly but always distinctly in spore accumulations after several hours of exposure) pseudoamyloid, without distinct germ pore, without noticeable metachromatism in cresyl blue; stipe

mostly annulate, probably in some (undescribed) species also with basal volva, in very few species without any veil; lamellae always distinctly free; spore print not changing by dehydration from green to purple, white in the majority of species but also often cream color, light brown to « burnt umber » (Maerz & Paul) and perhaps sometimes bluish green or pink. On the ground and on living and dead host plants, in deep moss, etc.

KEY TO THE GENERA

A Epicuticular layer of the pileus consisting of repent, filamentous hyphae, and hyphae of the trama amyloid, without clamp connections, veil obsolete or none. 88. *Pseudobaeospora*

A Epicuticular layer of the pileus not consisting of repent filamentous hyphae or hyphae of the trama not amyloid; clamp connections present or absent. 89. *Lepiota*

88. PSEUDOBAEOSPORA Sing.

Lloydia **5**: 129. 1942.

Type species: *Baeospora oligophylla* Sing.

Characters: Those of the tribus, but epicutis consisting of repent, clampless, hyaline, filamentous hyphae; trama consisting of amyloid, clampless hyphae; stipe elongate in deep moss, without any distinct annulus, or even veil; cystidia none; spores hyaline, small, globose, strongly pseudoamyloid.

Development of the carpophores: Unknown.

Area: Siberia (Altai Mts.).

Limits: This genus has initially been confused with the genus *Baeospora*. This latter genus has more elongate, amyloid spores and nonamyloid tissue. *Pseudobaeospora* is closely related to *Lepiota* whereas *Baeospora* is closely related to the *Marasmieae*, a tribus of the *Tricholomataceae* The limits to be discussed are not those between *Baeospora* and *Pseudobaeospora* but rather between *Pseudobaeospora* and *Lepiota*. In the latter genus, we know one aberrant section where the epicutis, according to reliable authors, consists of strictly repent hyphae like those of *Pseudobaeospora*. It is conceivable that this section will eventually be transferred to *Pseudobaeospora* but at present one would hesitate to set up a final delimitation since the reaction of the tissue of the Lepiotas in question has not been restudied, and their veil seems to be well developed, at least in certain

species. If the species with well developed veil should also have nonamyloid trama, one would be inclined to leave them in *Lepiota*, and restrict *Pseudobaeospora* to species corresponding to the diagnosis given above. If the context should turn out to be truly amyloid in the Lepiotas, the separation would probably be based on the microscopical and microchemical characters alone rather than on the veil.

The external appearance of *Pseudobaeospora* which is that of a *Collybia* rather than that of a *Lepiota*, and the characteristic pigmentation which is rare in the true Lepiotas, would also tend to provide additional characters; but in monotypic genera, it is necessary to avoid the mistake of considering too many specific characters as generic. Nevertheless, judging from what is now known in the taxonomy of the *Lepiotae*, the hiatus between *Pseudobaeospora* and *Lepiota* is very considerable.

State of knowledge : Only one species is known. It has been studied thoroughly by Singer (1938).

Practical importance : None.

SPECIES

P. oligophylla (Sing.) Sing. (Baeospora oligophylla Sing.).

89. LEPIOTA (Pers. ex) S. F. Gray

Nat. Arr. Brit. Pl. 1 : 601. 1821, em.

Type species : Lepiota colubrina (Pers. ex) S. F. Gray.

Syn. : Fusispora Fayod, *Ann. Sc. Nat., Bot.* VII. 9: 351. 1889 (descr. excl.).
Micropsalliota Hoehnel, *Sitz.-ber. Akad. Wiss. Wien, math.-nat. Kl.* 123 (1) : 79 [31]. 1914
Lepiotula R. Maire ex Locquin *Bull. Soc. Linn. Lyon* 14 : 28 [reprint pagination]. 1945.

Characters : Those of the tribus ; but hyphae of the epicutis rarely (if ever) repent and filamentous ; trama of the pileus rarely (if ever) amyloid ; hyphae with or without clamp connections ; habit characteristic because of the presence (in all ? — or at least most species) of a distinct annular veil, and scales of a micaceous or fibrous consistency, sometimes leaving a smooth disc (« calotte ») but the original entire cuticle breaking up all around the disk into fragments which are often deeper colored than the trama beneath and around

them; cystidia sometimes present on the sides of the lamellae but absent in the majority of the species; cheilocystidia mostly present. On the soil and on various other living and dead substrata (dead wood, ferns, shrub palms, fiber, straw, etc.).

Development of the carpophores. Hemiangiocarpous, according to Atkinson and Kuhner (*L. clypeolaria*, *L. cristata*, *L. seminuda*, *L. felina*).

Area: Cosmopolitan, but the single species with definitely smaller distribution. The largest assemblage of different species of this genus is found in Central and South America, and perhaps an equally large variety of forms can be expected in Africa, in the Pacific, and Southeast Asia. The temperate zone of North America is somewhat poorer in species, and Europe is much poorer in the number of species as well as in their abundance.

Limits: The delimitation of this genus has been under discussion for many years. All the other genera of the *Agaricaceae* except for *Agaricus* and *Cystoagaricus*, have at one time or another been considered as belonging in *Lepiota*, or else their characters are such that they were included in the older version of the diagnosis of *Lepiota*. Later, one genus after another was separated from *Lepiota* whereby the diagnosis of *Lepiota* became gradually emended, and the number of species restricted. The only genus which has formerly been split from *Agaricus*, viz. *Micropsalliota* Hoehnel, must be united with *Lepiota*. Otherwise, the diagnosis given above defines the genus *Lepiota* in the narrowest sense, i. e. approximately in the sense of *Lepiotula* R. Maire apud Locquin. The latter generic name is, however, not accepted because, for important practical reasons, the type species of *Lepiota* should be one within the genus *Lepiota* as outlined in the present work, not within one of the split groups

The separation between the genus *Pseudobaeospora* and *Lepiota* is based on the strongly amyloid trama, the repent filamentous epicuticular hyphae, and the absence of a veil. Locquin keys out a large and important group in *Lepiota* emphasizing their amyloid trama. The author knows only two of the species entering this group well enough to check upon this indication; one of the specimens re-examined has been received from Dr. Locquin himself. In both cases, the author was unable to confirm Locquin's statement. It is impossible to tell at the present moment what may have caused this discrepancy. Locquin also indicates for another group of *Lepiotas* what amounts to nonamyloid spores (i. e. non pseudoamyloid), or the equi-

valent of this in Locquin's terminology. Subdividing this same group in his key, he again admits pseudoamyloid spores for one of the subgroups, and nonamyloid spores for another. The author has examined, before and afterwards, numerous representatives of that group, even of the subgroup said to have nonamyloid spores, and all the species studied showed very clear to fairly clear positive reactions with Melzer's reagent in the sense of pseudoamyloid discoloration. Here again, it is impossible to state just what factor caused the discrepancy.

There is one section, consisting of a stirps of closely related species, not recently restudied by the author, which are said to have an epicutis consisting of strictly repent, smooth, filamentous hyphae in a radial arrangement. Macroscopically, they are neither squamose, nor woolly, nor even furfuraceous or micaceous, but sericeous. This section is amitted on a tentative basis, at the end of the classification of the gēnus *Lepiota* as envisaged by the author, but with the understanding that it may be transferred to *Pseudobaeospora* if the trama should turn out to be strongly amyloid and clamp connections lacking.

Lepiota seminuda and *L. rufipes* in the sense of Kühner might cause difficulties in the future because they are, according to Kühner, the only species of *Lepiota* (i. e. *Lepiota* in the widest sense, and we may safely substitute: the *Agaricaceae*) with uninucleate spores. The same author indicates that these two species can be mistaken one for another, and are very similar, yet, in his classification, Kühner puts them in different sections. In the following classification of *Lepiota* the author has omitted *L. rufipes*, and has put *L. seminuda* in the section *Micaceae* but this disposition of these species is tentative and temporary. It is quite possible that future taxonomists will put both species in a separate genus or subgenus.

As for the tropical *Lepiotae*, we have no reason to assume that they will greatly upset our present generic limits and sectional divisions. This is shown by a complete study of all the species of *Lepiota* found in the tropical and subtropical part of the state of Florida and several South American and African types by Beeli and Singer. Nevertheless, it is still possible that some species now described as *Lepiota* are as different as *Smithiomyces* and *Ripartitella* proved to be. For that reason, the classification proposed below is not considered final, yet its use will demonstrate that it is natural and workable

form with that part of Kühner's classification that concerns the genus *Lepiota* in the narrower sense; but some details have been changed according to the author's experiences. If, against expectation, the colored spore print of some tropical species should be a character of more than specific value, new taxonomic arrangements will be necessary [110].

State of knowledge : The papers giving modern descriptions, or at least the essential data on *Lepiotae* treat only a small percentage of the species in this large genus. The number of species admitted below (24) on the basis of the author's experience does not give a correct impression of the real number of species in *Lepiota*. The older descriptions are frequently as worthless as the « classical » descriptions of *Mycena*, and even some of the latest notes do not contain all the information needed, or neglect certain aspects.

Practical importance : None of the species of *Lepiota* is used as food in any considerable quantity. The Lepiotas are also not expected to play an important rôle in forest biology, or in phytopathology. The most important fact in this connection is the presence, in *Lepiota*, of at least two poisonous species, and at least one of them seems to belong to the same group of poisonous plants as *Amanita phalloides*, i. e. the symptoms are phalloidic in most regards, and the poisonous substance is deadly.

SPECIES

Sect. 1. **MICACEAE** Lange (1935) (Subgenus *Micacystis* Locquin 1945). Epicutis of the pileus pseudoparenchymatic (cellular).

Type species : L. seminuda (Lasch) Gillet.

L. seminuda (Lasch) Gillet ; *L. microspora* (Ellis) Sing. According to Kühner also the following species : *L. Bucknallii* (Berk. & Br.) Sacc., *L. Hetieri* Boudier ; and according to Locquin also *L. Hetieriana* Locquin and *L. Langei* Locquin.

Sect. 2. **ECHINATAE** Fayod (1889) (Subgenus *Echinoderma* Locquin 1945 ; sect. *Acutesquamosae* Murr. 1914). Pileus spiny or woolly-spiny-squamose, the tips of the spines often consisting of spherocysts ; spores pseudoamyloid.

[110] An Argentine species, presumably undescribed, has a spore print corresponding to « burnt umber » (Maerz & Paul). Otherwise, it is close to the species of section *Anomalae* where at least one other species with colored spore print

Type species : *L. acutesquamosa* (Weinm.) Gillet.

L. acutesquamosa (Weinm.) Gillet with several varieties and forms ; *L. asperula* Atk.

Sect. 3. **AMYLOIDEAE** Sing. (1943). Pileus with strong woolly-spiny-squamose covering, similar to that of sect. 2 ; spores amyloid.

L. amyloidea Sing.

Sect. 4. **CRISTATAE** Kühner (1936) (Subgen. *Lepiotula* Locquin 1945). Cuticle of the pileus, at least on the disc, consisting of a hymeniform layer, ruptured into scales or areolae, or longitudinally split over most of the surface of the pileus.

Type species : *L. cristata* (A. & S. ex Fr.) Quél. sensu Pat.

L. micropholis (Berk. & Br.) Sacc. sensu Locquin ; *L. lilacea* Bres. ; *L. cristata* (A. & S. ex Fr.) Quél. sensu Pat.

Sect. 5. **PILOSELLAE** Kühner (1935). Cuticle of the pileus with a palisade as the uppermost layer ; stipe entirely and evenly pilose ; context becoming green (or blue) with ammonia.

L. Georginae (W. G. Smith) Sacc.

Sect. 6. **STENOSPORAE** (Lange) Kühner (1936). Cuticle of the pileus as in the preceding section ; stipe not entirely pilose ; spores more or less distinctly « spurred » (i. e. with a protracted spur like angle on the lower outer side when seen in profile, or at least strongly truncate at the lower end).

Type species : *L. pseudofelina* Lange.

L. pseudofelina Lange ; *L. griseocirrus* R. Maire ; *L. Grangei* (Eyre) Lange ; *L. castanea* Quél. ; *L. ignicolor* Bres. ; — according to Kühner also *L. subalba* Kühner, *L. fulvella* Rea. and *L. tomentella* Lange.

Sect. 7. **CLYPEOLARIAE** (Fr.) Quél. (1872) sensu str. Kühner (1936). Cuticle of the pileus as in the two preceding sections ; stipe not entirely pilose, often beset with colored scales, or with the fragments of an obsolete evanescent annulus ; spores not « spurred », fusoid, 8.8-16 × 4 8 μ, rarely larger, never smaller.

Type species : *L. clypeolaria* (Bull. ex Fr.) Quél.

L. alba (Bres.) Kühner ; *L. metulispora* (Berk. & Br.) Sacc. ; *L. clypeolaria* (Bull. ex Fr.) Quél. ; *L. floralis* (Berk. & Rav.) Sacc. ; according to Kühner also *L. laevigata* Lange and *L. subgracilis* Kühner : according to Locquin also *L. ochraceosulphurescens* Locquin and *L. granulopunctata* Locquin ; apparently also *L. pallida* Locquin.

Sect. 8. **OVISPORAE** (Lange) Kühner (1936). Characters of the

annulus well developed or obsolete and fugacious, usually not funnel-shaped; clamp connections present.

Type species : L. subincarnata Lange.

L. subincarnata Lange; *L. pseudohelveola* Kühner; *L. felina* Quél.; *L. rubella* Bres.; aside from these species, Kühner indicates *L. parrannulata* (Lasch) Gillet, *L. citrophylla* (Berk. & Br.) Sacc.; *L. setulosa* Lange, *L. clypeolarioides* Rea, and *L. brunneoincarnata* Chodat & Martin; Locquin adds *L. Barlaeana* Pat., *L. helveola* Bres. sensu Josserand, *L. rhodorhiza* Romagnesi & Locquin, and *L. ? gracilis* Peck. Locquin puts *L. parrannulata* (Lasch) Gillet into a special subsection *Subalbae* Locquin where he also places « *L. ermiaca* aut. nonn. ». This latter group is unknown to the author.

Sec. 9. **ANOMALAE** Locquin (1945). Approximately same characters as in the preceding section but hyphae without clamp connections.

Type species : L. fuscovinacea Møller & Lange.

L. fuscovinacea Møller & Lange; *L. pseudovolvulata* (Höhnel) Sing. (Micropsalliota, Höhnel).

Sect. 10. **SERICELLAE** Kühner (1936). Cuticle of the pileus consisting of radially arranged fibrils which are appressed (repent), surface of the pileus white, sericeous.

Type species : L. serena (Fr.) Sacc.

Kühner indicates here, aside from the type species: *L. cygnea* Lange, and a species different from *L. serena* (Fr.) Sacc. which he temporarily names *L. serena* sensu Lange.

Note : This section has been added on a temporary basis (see p. 438 and p. 440).

KEY TO THE SPECIES

As for keys, the reader is referred to the existing special literature in Europe to Kühner, *Recherches sur le genre Lepiota. Bull Soc Myc Fr.* **52** : 187. 1936, also Locquin (*Bull Soc Linn Lyon* **14** : 30 1945). In North America, such general treatments as *North American Flora*, 48. *Lepiota* (by W. A Murrill, **10** : 42. 1914), and Kauffman, especially, *The Genus Lepiota in the United States, Pap. Mich Acad. Sc Arts Lett* **4** : 311-344. 1924, can be used for species identification. Rick has compiled the descriptions of Brazilian Lepiotas in *Lilloa* **1** : 308-346 1937.

GENERA INCOMPLETELY KNOWN

Schulzeria Bres., *Schulzeria*, *Nuov. Gen.*, p. 7. 1886. « White spored agarics without volva and annulus ; lamellae rounded behind, free, remote ; spores obovate, hyaline. (Exannulate Lepiotas, or white-spored *Plutei* or *Pilosaceae*) » Bresadola. The type species is *S. rimulosa* Schulzer & Bres. apud Bres. from Yugoslavia. The pictures and the original description published by Bresadola are taken from the original illustration and notes by Schulzer ; consequently Bresadola had no other part in it than to publish the material under a new generic name. One of Bresadola's comparisons, viz. « *Lepiotae* without annulus », seems to be most characteristic for the fungi in question. If the data published could be taken at their face value, it might certainly be possible to speak of a genus close to *Lepiota* but without annulus. However, it is not quite certain that Schulzer's spore measurements were correct. The small spores without a germ pore would exclude *Leucoagaricus*. It may be assumed that Schulzer overlooked the germ pore if one was present. As for the veil, its complete absence in specimens of the size of these Schulzerias would undoubtedly be remarkable were it not for the fact that it may have been overlooked because the specimens were too old, or because the annulus mobilis had slid down the stipe without having been noticed by Schulzer. Schulzer's own publications are not too reliable as far as exactitude of observation is concerned, and the same shortcoming may be attributed to the material sent to Bresadola. Since there is at present no way to prove either the correctness or the faultiness of Schulzer's observations, the genus *Schulzeria* is here listed as incompletely known, yet the author tends to believe that it refers to a mutilated, misrepresented *Leucoagaricus* or perhaps *Lepiota* rather than an autonomous genus of the *Lepioteae*. However, there seems to be at least one species (*S. flavidula* Rick ?) which agrees with the generic diagnosis but is not generically identical with any of the known genera (see key p. 411).

Tribus CYSTODERMATEAE Sing.

Type genus : *Cystoderma* Fayod.

Characters : Spores with simple or seemingly simple, rather thin walls and without germ pore, smooth, or more rarely echinulate, non-

amyloid or amyloid, or more rarely slightly pseudoamyloid (but then lamellae adnato-decurrent); spore print white to ochraceous; cup-shaped volva never present; lamellae either free, or adnexed to adnate (and often separating from the apex of the stipe), or rarely decurrent, consequently the habit not always pluteoid, but the general appearance of the carpophores strongly reminiscent of *Lepiota*; context consisting of hyphae with clamp connections.

KEY TO THE GENERA

A. Lamellae free; spores nonamyloid; epicutis hymeniform, or velar covers of the pileus heteromerous
  B. Spore print light ochraceous; epicutis hymeniform; cystidia conspicuous on the sides of the lamellae — 91. *Drosella*
  B. Spore print pure white; epicutis not hymeniform; velar layer of the pileus heteromerous; cystidia none — 92. *Smithiomyces*

A. Lamellae not free; spores nonamyloid, or amyloid, or slightly pseudoamyloid; epicutis not hymeniform; velar layer not heteromerous but, if present, consisting either predominantly of hyphae or predominantly of sphaerocysts.
  C. Uppermost layer of the pileus an epithelium, more rarely absent, and the cuticle then irregularly intermixed, but if the epithelium is absent on the pileus, it is at least present on the stipe; spores smooth; stipe never distinctly eccentric in normally developed specimens
    D. Spore print white in mass, or nearly so, never ochraceous; spores completely smooth, without conspicuous or persistent perisporium. — 92. *Cystoderma*
    D. Spore print ochraceous; spores often faintly punctulate, and with a rather persistent perisporium. — 93. *Phaeolepiota*
  C. Uppermost layer of the pileus a trichodermium; stipe not covered by an epithelium; spores echinulate, small, subglobose; stipe often somewhat eccentric. — 94. *Ripartitella*

90. DROSELLA R. Maire apud Kühner & Maire

Bull. Soc. Myc. Fr. **50**: 15. 1934.

Type species: *Drosella irrorata* (Quél.) Kühner & Maire.

Syn.: *Lepiota* subgenus *Lepiotella* Gilbert, *Le Genre Amanita Persoon*, p. 159. 1918.
Lepiotella (Gilbert) Gilbert ex Kühner & Maire, *l. c.*; Singer, *Ann. Mycol.* **34**: 338. 1936 [444]).

[444] The fact behind this citation — difficult to express in the routine formula

Characters : Pileus somewhat fleshy, with hymeniform epicutis; lamellae free but not remote from the stipe; spore print ochraceous-cream; spores subhyaline, without germ pore, nonamyloid (also not pseudoamyloid), smooth, small; cystidia conspicuous on the sides of the lamellae as well as on the edges; context nonamyloid, consisting of hyphae with clamp connections. On the ground and on very decayed wood.

Development of the carpophores : Unknown.

Area : Europe.

Limits : These are clear from the characters indicated in the key and in the generic diagnosis.

State of knowledge : Only one species is known.

Practical importance : *D. fracida* is edible but not very important because of its scarcity, and the low quality as food.

SPECIES

D. fracida (Fr.) Sing. (Armillaria, Sacc. [2]); Lepiota irrorata Quél.; Drosella, Kühner & Maire; Lepiotella, Sing.)

91. SMITHIOMYCES Sing.

Mycologia 36: 366. 1944

Type species : *Leucomyces mexicanus* Murr.

Characters : Pileus covered with extremely thin fragments of a membranous veil which consists of a tissue of heteromerous structure (spherocysts scattered among filamentous hyphae), smooth, naked except for the veil, dry; lamellae free, eroded; spore print pure white; spores hyaline, smooth, small, neither amyloid nor pseudoamyloid, without germ pore, with a rather thin and seemingly simple wall; cystidia none; hymenophoral trama subregular, not bilateral; stipe with a distinct annulus and an inconstant, rudimentary

group under the generic name *Lepiotella* sixteen years before R. Maire did. Kühner & Maire as well as Singer did not check upon this claim — Gilbert's booklet on the Amanitas is rather rare — and accepted this statement. Actually, however, Gilbert merely proposed a subgenus within *Lepiota*. There can be no doubt that under these circumstance *Drosella* Maire is the legal name for the genus

volva ; context soft, fleshy, white ; tissue nonamyloid ; hyphae with clamp connections. The carpophores are often reminiscent of the white Amanitas. On the ground and on very decayed wood.

Development of the carpophores : Unknown, probably hemiangiocarpous.

Area : Florida to Brazil, and east to Mexico.

Limits : The characters as indicated in the key characterize this genus sufficiently.

State of knowledge : Only one species is known.

Practical importance : None.

SPECIES

S. mexicanus (Murr.) Sing. (Leucomyces, Murr. ; Amanita, Murr. ; Venenarius, Murr.).

92. CYSTODERMA Fayod

Prodrome, *Ann. Sc. Nat., Bot.* VII. 9: 351. 1889

Type species : *Agaricus amianthinus* Scop. ex Fr.

Characters : Both stipe and pileus in the mature stage covered with a velar layer or epicutis which consists predominantly of sphaerocysts (epithelium), the epithelium often strongly intermixed with elongate elements, but in other cases almost purely pseudoparenchymous ; rarely only the stipe with a cellular covering ; lamellae adnexed, adnate, sometimes even subdecurrent with a tooth, sometimes sinuate, sometimes separating from the stipe in age ; hymenophoral trama regular to subregular ; spore print white ; spores hyaline, smooth, ellipsoid to subglobose or ventricose to subrhomboid in outline, either amyloid, or nonamyloid, or weakly pseudoamyloid (after long exposure) ; cystidia sometimes present ; stipe with indistinct annulus, annulus more rarely very well developed, flaring ; context fleshy, soft, watery ; tissue nonamyloid ; hyphae with clamp connections. On moss, on the ground, or on rotten wood.

Development of the carpophores : Probably always hemiangiocarpous (known to be in *C. granulosum,* Kühner 1926).

Area : Cosmopolitan, but fewer species in the tropics than in temperate climates.

Limits : Some mycologists including Fayod himself, also Singer

(1936 1943), have considered all *Agaricaceae* (except those with a germ pore) with ephitelium as belonging to *Cystoderma*. However, Konrad & Maublanc, and later Smith & Singer emended the genus, and excluded the species with truly free lamellae and distinctly colored or distinctly pseudoamyloid spores. The genus *Phaeolepiota* which is the only other genus in this tribus with a well developed ephithelium on pileus and stipe, differs in the color of the spores and in their slight punctation in many spore prints. *Ripartitella* differs in the structure of the surface layers of both pileus and stipe, in the small, round, echinulate spores, and in the *Melanoleuca* cystidia. The light-spored *Phaeomarasmii* have a very different type of cheilocystidia.

State of knowledge : A monographic study has been published on this genus by Smith & Singer, *Pap. Mich. Acad. Sc., Arts, Lett.* **30** : 71-124, pl. I-V. 1945. The genus can be considered as comparatively well known. Fifteen species are now recognized.

Practical importance : None.

SPECIES

Subgenus I. **Eucystoderma** Sm. & Sing. Uppermost layer of the mature pileus formed by an epithelium ; spores either nonamyloid, or amyloid, or very weakly pseudoamyloid, small, rarely medium sixed ; lamellae rarely arcuate and adnato-decurrent.

Type species : C. amianthinum (Scop. ex Fr.) Fayod ex aut.

Sect. 1. GRANULOSA (Fr.) Locquin em. Locquin (1945), Sm. & Sing. (1945). Spores nonamyloid, or sometimes extremely weakly pseudoamyloid.

Type species : C. granulosum (Batsch ex Fr.) Fayod ex aut.

C. Ambrosii (Bres.) Sm. & Sing. (Armillaria, Bres.); *C. granulosum* (Batsch ex Fr.) Fayod ex aut. (Lepiota, S. F. Gray) and var. *occidentale* A. H. Smith apud Sm. & Sing. and var. *adnatifolium* (Peck) Sm. & Sing. (Lepiota adnatifolium Peck) ; *C. ponderosum* Sm. & Sing. ; *C. cinnabarinum* (A. & S. ex Secr.) Fayod ex aut. (Lepiota, Karst. ; Lepiota granulosa var. cinnabarina Gillet) ; *C. australe* Sm. & Sing. ; *C. rhombosporum* (Atk.) Sm. & Sing. (Lepiota, Atk.).

Sect. 2. AMIANTHINA Sm. & Sing. (1945) (*Genuinae* Locquin 1945, nom. subnud.). Spores amyloid.

Type species : C. amianthinum (Scop. ex Fr.) Fayod ex aut.

pulveraceum (Peck) Sm. & Sing. (Lepiota, Peck); *C. caucasicum* Sing. apud Sm. & Sing.; *C. amianthinum* (Scop. ex Fr.) Fayod ex auct. (Lepiota, Karst.) with var. *sublongisporum* Sing. and var. *longisporum* (Kühner) Sm. & Sing.; *C. fallax* Sm. & Sing.; *C. granosum* (Morgan) Sm. & Sing.; *C. subvinaceum* A. H. Smith apud Sm. & Sing.; *C. haematites* (Berk. & Br.) Kühner & Maire.

Subgenus II. **Dissoderma** Sm. & Sing. Mature pileus without epithelium; cuticle of the pileus consisting of irregularly interwoven intermixed hyphal elements, some of them rather swollen, others filamentous; spores weakly pseudoamyloid, medium sized (9.5-11 µ long); lamellae arcuate and adnato decurrent.

C. paradoxum Sm. & Sing.

KEY TO THE SPECIES

A. Spores nonamyloid, or weakly pseudoamyloid
- B. Mature pileus without an epithelium — *C. paradoxum*
- B. Mature pileus with an epithelium
  - C. KOH not coloring the cuticular cells or the pileus, or if so, only a pale yellowish tint developing. — *C. Ambrosii*
  - C. KOH causing the cuticular cells to become tawny to deep rusty brown or reddish
    - D. Spores ellipsoid to subglobose
      - E. Hypodermial cells (elongate elements forming a layer just below the epithelium) without conspicuous incrusting pigment, the pigment being localized in the cell wall.
        - F. Cheilocystidia absent. — *C. granulosum*
        - F. Cheilocystidia present.
          - G. Carpophores terrestrial, large, fleshy, pileus usually cinnabar red to orange. Circumpolar. — *C. cinnabarinum*
          - G. Carpophores lignicolous, small; pileus rusty brown. Florida. — *C. australe*
      - E. Hypodermial cells, and cells of the epithelium with an incrusting pigment which is distinctly seen when the material is revived in KOH. — *C. ponderosum*
    - D. Spores subrhomboid to ventricose apiculate. — *C. rhombosporum*

A. Spores amyloid.
- H. KOH not coloring the cells of the cuticle
  - I. Carpophores terrestrial; cuticular cells without filamentous proliferation. — *C. carcharias*
  - I. Carpophores lignicolous; cuticular cells sometimes proliferated. — *C. pulveraceum*
- H. KOH coloring the cuticular cells.
  - J. Discoloration caused by KOH in the cuticular cells tawny, rusty, or reddish.

K. Brownish pigment dissolved in the cell sap in at least some cells. Caucasus. *C. caucasicum*

K. Pigment localized in the cell walls.

L. Spores usually 5 or more µ long *C. amianthinum*

L. Spores usually shorter than 5 µ.

M. Pileus 20-50 mm broad; carpophores terrestrial, usually under conifers; cheilocystidia none. *C. fallax*

M. Pileus 40-90 mm broad; carpophores growing on decaying hardwood logs; clavate cheilocystidia present. *C. granosum*

J. Discoloration caused by KOH in the cuticular cells olive gray.

N. Lamellae unchanging when bruised; context of pileus and stipe pallid; on decaying wood in North America. *C. subrinaceum*

N. Lamellae white, becoming reddish when bruised (according to Rea), context pale liver color, yellowish in the stipe (according to Rea), carpophores terrestrial in Europe. *C. haematites*

93. PHAEOLEPIOTA R. Maire

Bull. Soc. Mycol. Fr. **27**: 39. 1911 (nom. nud.) ex Konr. & Maubl., *Icon. Sel. Fung.* **6**: 111. 1924-38.

Type species: *Pholiota aurea* (Mattuschka ex Fr.) Gillet.

Characters: Pileus and stipe and the lower surface of the broad, flaring membranous annulus covered with a loose mealy easily removable substance consisting of sphaerocysts (an epithelium); lamellae adnexed; spore print light fulvous-melleous or ochraceous; spores under the microscope rather pale yellowish, stramineous, smooth or indistinctly punctulate in many mature walls, and besides often with a perisporial covering, elongate (guttiform oblong to amygdaloid), with suprahilar depression, medium sized to large, nonamyloid; basidia normal in all regards; cystidia none, even on the edges; hymenophoral trama of young carpophores regular or almost so; stipe central, annulate; context in the pileus and in stipe thick, fleshy; tissue nonamyloid; hyphae with clamp connections. On the ground in woods.

Development of the carpophores: Hemiangiocarpous.

Area: Temperate (western North America, large parts of extratropical and subtropical Asia and Europe); specimens from South America proved to be something else.

Limits: This is closest to, though well separated, from *Cystoderma*. The size, wall structure, and color of the spores is different in *Cystoderma* and *Phaeolepiota*.

State of knowledge : The only species referable to this genus is well known.

Practical importance : *P. aurea* is edible.

SPECIES

P. aurea (Mattuschka ex Fr.) R. Maire ex Konr. & Maubl. [Pholiota, Gillet ; Togaria, W. G. Smith ; Pholiota Vahlii (Schum. ex Fr.) Lange ; Lepiota pyrenaea Quél.].

94. RIPARTITELLA Sing.

Mycologia 39 : 85. 1947.

Type species : Ripartitella squamosidisca (Murr.) Sing. (= *R. brasiliensis*).

Characters : Habit of the carpophores reminiscent of *Lepiota* but with the lamellae variably attached, and the stipe sometimes more or less eccentric : pigment rusty, incrusting the walls of the hyphae; pileus squamulose, the squamules consisting of somewhat intermixed, dense chains of short hyphal members which are almost isodiametric to elongate and cylindric but do not assume the shape of spherocysts; lamellae adnate to emarginate or separating from the apex of the stipe, or decurrent with a tooth; spore print white or nearly so; spores hyaline, echinulate, ellipsoid to subglobose, much like those of *Clitocybe inversa*, nonamyloid, without germ pore ; basidia normal, 4 spored ; cystidioles very conspicuous in most specimens, strongly reminiscent of those of *Melanoleuca,* hyaline, thin-walled to medium thin walled, with crystalline, sagittate incrustation above, ampullaceous or subulate, on the sides of the lamellae as well as on the edge, trama of the hymenophore regular, hyaline, consisting of thin-walled hyphae ; stipe often eccentric, indistinctly or distinctly veiled but annulus rarely developed ; base with short white strands of rhizomorphs (as, for that matter, in many *Agaricaceae*) ; context fleshy, consisting of hyphae with clamp connections and nonamyloid walls ; on the ground and on decaying wood.

Development of the carpophores : Unknown, probably hemiangiocarpous.

Area : Subtropical and tropical America from Florida to Brazil.

Limits : This genus has distinctly the habit and the pigmentation

of *Cystoderma*. The cystidia — though primarily reminiscent of those of *Melanoleuca* — are also comparable with the cystidia of *Cystoderma cinnabarinum*. The general appearance is that of a *Lepiota*. It differs from all other genera of *Agaricaceae* in the characteristic echinulate spores. In this latter regard one is tempted to compare *Ripartitella* with *Ripartites*. However, *Ripartites* differs in colored spore print, in different characters of the surface of the pileus, in the lack of the cystidia, and in the persistently decurrent lamellae.

State of knowledge: Only one species is known. This has been redescribed by Singer, *Lloydia* **9**: 127-128. 1946.

Practical importance: None.

SPECIES

R. brasiliensis (Speg.) Sing. (Pleurotus, Speg.; Marasmius squamosidiscus Murr.; Ripartitella, Sing.).

COPRINACEAE Roze

Bull. Soc. Bot. Fr. **23**: 51. 1876, nom. nud.; l. c. p. 111. 1876 (ut Coprinidées); Heim, *Treb. Mus. Ciènc. Nat.* Barcelona **15**: 130. 1934.

Type genus: *Coprinus* (Pers. ex) S. F. Gray.

Syn.: *Scotosporaceae* Romagnesi, *Rev. Mycol.* **2**: 23. 1937 (nom. nud.

Characters: Hymenophore lamellate; the lamellae of the *Coprinus*-type (with parallel or subparallel sides) or wedge-shaped of the aequihymeniiferous or the inaequihymeniiferous type; in the genera with aequihymeniiferous and wedge-shaped lamellae — epicutis of the pileus always characteristically cellular, the epicutis often consisting of somewhat compressed (not always quite globose) but distinctly subisodiametric bodies which are often somewhat colored, or arranged in chains but not mealy in most species, rather rarely covered up by a velar layer which consists of elongate elements; otherwise, i. e. if the lamellae are of the inaequihymeniiferous type or with parallel or subparallel sides, they usually tend to deliquesce, and in extreme cases which are rather common, the whole pileus eventually deliquesces, the drops formed being black in the majority of cases, more rarely fuscous, etc. (according to the color of the spores in mass), and white in sterile specimens; spores, where obtainable

in print, usually dark colored : black, dark fuscous, purplish fuscous, rarely as light colored as dull purplish lilac or russet-lilac, or brick-russet ; individual spores rather dark colored under microscope in most species, more rarely light colored, usually with distinctly double or even more complex wall, with, rarely without, a well developed germ pore, smooth, rarely warty, echinate, reticulate or otherwise ornamented, globose, ellipsoid, cylindric-oblong, almond-shaped, lemon-shaped, angular, the smaller diameter (breadth) usually equal in all positions, more rarely compressed as in *Deconica*, rather small to very large, sometimes in different sizes according to the age-group of basidia from which they were discharged ; basidia normal but rather short and broad in many species ; lamellae free to subdecurrent, in the species without volva and with non deliquescent lamellae never quite free ; hymenophoral trama regular, becoming subregular in age ; stipe central, with or without veil ; context somewhat dry as in the *Gastromycetes* when mature, or usually fleshy to membranous, often very fragile ; tissue consisting of hyphae with or rarely without clamp connections. On various substrata, frequently on the earth, or on humus, or on dead wood, or on dung, or on fallen leaves, or on sand, in and outside the woods, often in buildings, in greenhouses, etc., even parasitically on other agarics or on various Cormophytes.

Limits : The *Coprinaceae* are here restricted to the three subfamilies *Coprinoideae*, *Psathyrelloideae*, and *Panaeoloideae*. These three subfamilies as a unit, are very natural and closely related to each other. They differ from all the other dark spored agarics by either having the *Coprinus* type of hymenophore or having a cellular epicutis. Aside from that most normal forms have clamp connections, and the spores are usually provided with a germ pore and are dark (not bright colored or pale) in a good print. In fact, it appears that the *Coprinaceae* are more closely related to the *Agaricaceae* and the *Bolbitiaceae* than to any of the other dark spored groups. As for the delimitation of the *Coprinaceae* from the latter two families, the reader is referred to the corresponding paragraph under the *Agaricaceae* and under the *Bolbitiaceae*.

Phylogeny : The family *Coprinaceae* is closely connected — by the way of slow intergrading — with certain gastroid genera, especially *Montagnea* Fr. The whole family is a steady transition from the gastroid to the agaricoid type of basidiomycetes, forming a series starting with such fully agaricoid groups as *Panaeolus*, through half

coprinoid groups like *Pseudocoprinus* into truly coprinoid groups like most species of the present genus *Coprinus* and from there to a genus halfway between the *Coprini* and *Montagnea*, viz. Maire's *Xerocoprinus*. From here to *Montagnea* it is only a small step. The author does not think that the families closest to this, i. e. the *Agaricaceae* and the *Bolbitiaceae* have developed directly from or into the *Coprinaceae*. Rather, it would seem that they are parallel branches. Just where the branching off has taken place, is impossible to state without taking sides in a theoretical controversy which would merely provide an a priori decision.

KEY TO THE SUBFAMILIES

A. Sides of the lamellae parallel or subparallel; pileus often deeply plicate at least near the margin, hymenophore and margin, or even the whole carpophore, often deliquescent. *Coprinoideae*.

A. Lamellae more or less wedge-shaped in cross section, i. e. acuminate toward the edge, the sides not parallel, non deliquescent.

B. Spores discolored with concentrated H_2SO_4 to pale slate color, even if they were black and opaque when seen in water. *Psathyrelloideae*.

B. Spores not discolored in H_2SO_4. *Panaeoloideae*.

Subfamily **Coprinoideae** (Fayod) Sing.

Ann. Mycol. **34**: 339. 1936

Type genus: *Coprinus* (Pers. ex) S. F. Gray.

Syn.: *Coprinoideae*, Fayod, *Ann. Sc. Nat., Bot.* VII. **9**: 379. 1889 (ut subtribus). *Coprineae* Henn., in Engl. & Prantl, *Nat. Pfl.-fam.* I. 1**: 204. 1898, em. Heim, *Treb. Mus. Cien. Nat.* Barcelona **15**: 132. 1934 (ut tribus).

Characters: Sides of the lamellae parallel; hymenophore of the inaequihymeniiferous type, or else with dry, somewhat toughish consistency and lamellae subdeliquescent; epicutis not always cellular often in hyphal chains, or merely radially fibrillose, or with a dichophysoid structure, etc.; hyphae with, or more rarely without clamp connections (probably all «normal», i. e. heterothallic tetrasporous races, with clamp connections, but the species very variable in their sexuality). On the soil, or on various other substrata.

KEY TO THE GENERA

A Pseudoparaphyses and basidioles in the young carpophores irregularly distributed and consequently not forming a hymenium of the true *Coprinus*-type; lamellae not distinctly deliquescent; context somewhat toughish as in some *Gastromycetes* (such as *Galeropsis*, *Montagnea*, *Battarraea*, etc.)
95. *Xerocoprinus*.

A. Pseudoparaphyses and basidioles in the young carpophores regularly distributed and consequently the lamellae of the typical inaequihymeniiferous pattern, strongly deliquescent in most species under normal circumstances; context fleshy or very thin and fragile 96. *Coprinus*

95. XEROCOPRINUS R. Maire

Bull. Soc. Bot. Fr. 7: ccxiv. 1907.

Type species: *X. arenarius* (Pat.) R. Maire.

Characters: Those of the subfamily, but lamellae only subdeliquescent or non-deliquescent at maturity; pattern of the hymenium not corresponding to that of the inaequihymeniiferous forms; annulus and volva present; cystidia none; context somewhat toughish as in many *Gastromycetes* such as *Galeropsis*, *Montagnea*, *Battarraea*, etc. In deserts.

Development of the carpophores: Not studied.

Area: Sahara and adjacent dry regions of Africa.

Limits: The subdeliquescent lamellae, the consistency of the flesh, the presence of a volva and an annulus, and the inaequihymeniiferous type of hymenophore characterize this genus well enough.

State of knowledge. *Pseudocoprinus arenarius* has not been restudied since Patouillard and R. Maire (1892 and 1907 respectively), and it would be desirable to learn more about this remarkable genus, especially in the light of the investigations of Buller, Kühner, and Romagnesi, also about the individual development of the carpophores and the hymenophore which is presumably born angiocarpously. The genus is admitted here on an equal level with *Coprinus* and other well known genera because of the detailed data given by R. Maire on certain vital parts of the description which cannot but confirm Maire's belief in the autonomy of this desert form. Only one species is known.

Practical importance: None.

SPECIES

X. arenarius (Pat.) R. Maire (Coprinus, Pat.).

96. COPRINUS (Pers. ex) S. F. Gray

Nat. Arr. Brit. Pl. **1** : 632 1821.

Type species : *C. comatus* (Müller in Fl. Dan. ex Fr.) S. F. Gray.

Syn. : *Pranulus* Ces. ex S. F. Gray, *l. c.*, p. 630
Onchopus Karst., *Bidr. Finl. Nat. Folk* **32** : xxviii 1879.
Pselliophora Karst., *l. c.*
Coprinellus Karst., *l. c.*
Coprinopsis Karst., Hymenomycetes Fennici, *Acta Flor. faun. Fenn.* **2** (1) : 27. 1881.
Oncopus Karst., *Basidsc.*, p. 256 1889 (spelling variation of *Onchopus* Karst.).
Lentispora Fayod, Prodrome, *Ann. Sc. Nat.*, *Bot* VII. **9** : 379. 1889.
Ephemerocybe Fayod, *l. c.*, p. 380.
Annularius Roussel ex Earle, *Bull. N. Y. Bot. Gard.* **5** : 443. 1909.

Characters : Pileus usually conical or campanulate in youth, more rarely initially subglobose, then expanding in many species, especially in the small ones; structure of the epicutis and velar layers very varied; margin (or often the entire pileus except for the narrow disc) frequently deeply plicate-furrowed along the back of the lamellae which have parallel sides (Pl. XX, 3) and disappear in age by autodeliquescence starting from the edge upwards, free or sinuate, or adnexed, or adnate; hymenium consisting of isolated basidia (Pl. XII, 1) arranged rather regularly according to stage of development among sterile cells — pseudoparaphyses — and consequently offering a checkers-like aspect when looked at under low power at the time when the spores begin to mature; characteristic large cystidioles very frequently present on the sides of the lamellae (Pl. XX, 3); cheilocystidia proper not differentiated in most species but the edges of the lamellae of the heteromorphous because of the presence, there, of large, loosely attached spherocysts; spore print black or fuscous; spores under the microscope blackish and opaque (Pl. XII, 1), more rarely fuscous and opaque, or transparent, but always very deeply colored by a pigment which can easily be extracted and destroyed by concentrated sulphuric acid, leaving the spore wall pale slate color, with germ pore, smooth, more rarely warty, echinate, reticulate, or angular, frequently compressed from both the inner and outer side to become approximately lentiform as the spores of *Deconica*, axially asymmetric and sometimes almost completely asymmetric, with complex wall, the perisporium often comparatively persistent; basidia

normal but rarely clavate, usually cylindric or even narrowed in the middle, (1) 2-(3)-4 spored; hymenophoral trama regular; stipe central and more or less straight; veil present or absent, and, if present, often indistinctly double, often condensed into an annulus, or with an annulus in the lower part of the stipe and the veil then resembling a volva, usually also apparent on the pileus (floccons, etc.), rarely with a true, well developed cup-shaped volva at the base; context usually white or whitish, fleshy, or very thin and fragile to almost absent in the tiniest species and specimens; clamp connections more often present than absent, and perhaps always present in the normal forms. On dung, or on soil, sand, peat, on various fabrics, on living *Basidiomycetes,* around living tree trunks, on dead wood, etc., also in buildings, often in greenhouses, on charcoal, in and outside the woods; often forming small sclerotia.

Development of the carpophores: Mostly or always hemiangiocarpous; for more details see the comprehensive paper by Chung Hwang Chow, *Contribution à l'Etude du developpement des Coprins. Le Botaniste* **26**: 89-236. 1934, also Atkinson (1916), Levine (1914), and Kühner (1926).

Area: Cosmopolitan.

Limits: The autodeliquescence of the lamellae can almost always be observed where true *Coprini* grow under optimal conditions. This, combined with the peculiar type of hymenophore and hymenium should make it rather easy to distinguish *Coprinus* in all cases.

State of knowledge: The genus *Coprinus* has not been studied satisfactorily in a monographic paper whose primary subject is the taxonomy of the genus. Some authors have contributed considerably to the present knowledge of the genus, but a monograph is still to be hoped for. On the other hand, the *Coprini* lend themselves easily to physiological and cytological studies, and many investigations — in fact all the classical contributions — on the sexuality of the agarics were made with material belonging to the genus *Coprinus,* and many generalizations in this field are mainly based on what has been observed in *Coprinus.* As for this phase of the investigations on *Coprinus,* the reader is referred to the following authors: Buller, Vandendries, Quintanilha, and Chung Hwang Chow — where many other papers have been summarized.

As for the taxonomy of the genus *Coprinus,* many species have still to be inserted in the present scheme, and a revision of the smaller units of the classification — (especially subsections), will become

necessary when a larger number of species is considered. *Coprinus* is actually one of the larger genera in the *Agaricales* — which does not find its true expression in the small number of species indicated by the author in the present work —, and it may be that future investigations in the anatomical and experimental field will tend to recognize natural groups with a strong hiatus between them — that may be considered as subgenera or genera rather than as sections. At present, the author does not feel competent to go as far as that.

Practical importance: The *Coprini* are easy to cultivate under usual laboratory conditions and therefore lend themselves better than most other agarics to all kinds of investigations, demonstrations and for a potential use in industry. It is unfortunately impossible to grow them for food because of the difficulty of transport. Their early autodeliquescence makes it practically impossible to have them in the market before they are « inky ». However, several species are harvested by amateurs every year as long as they are very young, and are considered as first class edible mushrooms. In this category belong especially *C. micaceus, C. comatus*, and *C. microrhizus. Coprinus atramentarius* is of lesser quality as far as taste is concerned, besides, French mycophagists claim that it is unwholesome, causing erythrism, if consumed before or after alcoholic beverages. This same species, however, is the main source of what is known as *Coprinus* ink, a suspension of the spores in water and several other ingredients. It has approximately the properties of Chinese ink, and is used for retouche work in photography, and in emergencies and for specific effects, in writing and drawing. The *Coprinus* ink has some future in police work since a given mixture of species would provide an easily recognizable ink in documents of importance.

Certain species of *Coprinus* are known to be « weed fungi » in the beds prepared for white mushroom growing. They develop faster than the *Agaricus* and appear before the first fruiting bodies of the latter can be harvested, sometimes even on the fermenting manure heaps before they are taken into the mushroom houses or cellars. Their influence on the production of carpophores by the *Agaricus* has been interpreted in different ways by different growers. The word « weed fungi » would imply a certain degree of competition for nutrition in the substratum, and a certain damage done to the mycelium of the *Agaricus* since it is deprived of optimum conditions long before it reaches the stage of fructification. On the other hand, practical experience shows that growers do not dread the appearance

of the *Coprini*, in the contrary, they are usually taken as a sign that the quality of the manure is good, and a normal harvest can be expected. A scientific approach to this problem would be desirable in the interest of the mushroom industry.

Another species of *Coprinus*, *C. radians* has proved to be responsible for the destruction of fabrics in the Pacific Islands. It must be asumed that this is only one of several species capable of inflicting damage to exposed clothing and equipment.

SPECIES

Sect. 1. **COMATI** Fr. (1838) em. Lange (1915) [*Pelliculosi* (Fr. 1838 ut tribus [113]) em. Schroter 1889]. Young pileus covered with a tomentum or with scales or fibrils, the tomentum, scales or fibrils formed exclusively by hyphal filaments, or else the pileus is without any macroscopical covering layer, and then the epicutis not cellular.

Type species : C. comatus (Muller in *Fl. Dan.* ex Fr.) S. F. Gray.

Subsection **Annulati** Lange (1915). Stipe with a distinct narrow annulus which is usually free or occasionally attached to the base of the stipe ; spores large, more rarely medium sized (10 25 µ in length) ; carpophores growing directly on dung or on manured ground, in ruderal places in gardens and parks, on lawns, etc.

Type species : Same as in the section.

C. comatus (Müller in *Flora Dan.* ex Fr.) S. F. Gray ; *C. sterquilinus* Fr.

Subsection **Atramentarii** (Fr. 1838 ut sect.) Konr. & Maubl. 1924 37. Veil indistinct, on stipe not distinctly annulate and never free ; spores usually smaller than 12 µ, sometimes with distinct ornamentation ; growing near trees.

Type species : C. atramentarius (Bull. ex Fr.) Fr.

C. atramentarius (Bull ex Fr.) Fr. ; *C. insignis* Peck ; obviously also *C. Romagnesianus* Sing. [C. atramentarius var. squamosus Bres. ; C. squamosus (Bres.) Romagnesi, non Morgan].

Subsection **Alachuani** Sing. Cuticle of the pileus made up by filamentous hyphae with small side branches and branchlets, often

[113] The *Pelliculosi* of Fries are termed a tribus, and correspond to what is otherwise considered as a subgenus by Fries The next lower unit — to which the *Comati* belong — is therefore the section, as understood by Fries and the modern taxonomists

branching off at an approximately right angle and forming a dichophysoid structure.

C. alachuanus Murr.

Sect. 2. **MICACEI** Fr. (1838) em. Schroter (1889) (*Farinosi* Lange 1915). Cuticle or veil made up partly or entirely of spherocysts or at least chains of isodiametric elements.

Type species : C. micaceus (Bull. ex Fr.) Fr.

Subsection **Domestici** Sing. (1948) Covering layer of the pileus formed not exclusively of spherocysts and isodiametric elements but the latter intermixed with a large number of fibrils and filaments.

Type species : C. domesticus (Bull. ex Fr.) S. F. Gray sensu Lange.

C. domesticus (Bull. ex Fr.) S. F. Gray sensu Lange ; also *C. radians* (Desm.) Fr. and many other species (see Romagnesi in *Rev. Myc.* **10** : 88. 1945).

Subsection **Exannulati** Lange (1915). Veil composed of spherocysts exclusively or with a few thin filamentous connective hyphae intermixed.

Type species : C. micaceus (Bull. ex Fr.) Fr.

C. micaceus (Bull. ex Fr.) Fr.; *C. niveus* (Pers. ex Fr.) Fr.; *C. curtus* Kalchbr. and many more species.

Each of the three species mentioned above may be considered as the central species of a stirps.

Subsection **Nudi** (Lange ut sectio [114] 1915). Veil usually macroscopically not visible; epicutis cellular.

C. plicatilis (W. Curt. ex Fr.) Fr.

Subsection **Auricomi** Sing. (1948). As the preceding subsection but with long hairs arising among the cells of the epicutis.

C. auricomus Pat.

KEY TO THE SPECIES

The author is unable to publish a better key to the species than that published by Kauffman for the flora of Michigan, U. S. A., Lange for Denmark, and Romagnesi for France. A combination of these keys should generally lead to the correct species or at least its neighborhood as long as temperate species are concerned. The species of the tropics cannot be determined by keys.

[114] There is certainly no need for the *Nudi* as a section. In fact, the author wonders if this subsection should not be combined with the preceding one because of the potential veil in *C. plicatilis*. The same is true for the subsection *Annulati* Lange (1915) which, by the way, is a synonym of the section *Cyclodei* Fr. (1838). The presence of an annulus is not more than a specific character.

Subfamily **Psathyrelloideae** (Kühner) Singer

Type genus : Psathyrella (Fr.) Quél.

Syn : Psathyrelles Kühner, *Bull. Soc. Myc. Fr.* **52** : 33 1936

Scotospores Romagnesi, *Revue de Mycologie* **1** (1) : 33. 1936 (ut series)

Scotosporaceae Romagnesi, *Rev. Myc.* **2** (6) 245 (ut familia, nom. nud.). 1937.

Scotosporoideae Sing., *Ann. Mycol.* **34** : 339. 1936 (ut subfamilia) ; trib. *Psathyrelleae* Romaguesi, *l. c.*

Characters : Lamellae wedge-shaped ; spores not discolored in H_2SO_4.

KEY TO THE GENERA

A. Pileus small, plicate-sulcate ; spore print black or deep fuscous ; hymenium of the *Coprinus* type (*Psathyrella*-subtype). 97 *Pseudocoprinus.*

A. Not combining these characters

B. A well developed, large cup-shaped membranous volva present at the base of the stipe. 98. *Macrometrula.*

B. Volva indistinct and fugacious, or none 99 *Psathyrella.*

97. **PSEUDOCOPRINUS** Kühner

Le Botaniste sér XX 155. 1928.

Type species : Agaricus disseminatus Pers. ex Fr.

Characters : « Pileus thin, membranous, very fragile, plicate-furrowed, split above the back of the lamellae as the pileus of the *Coprini Veliformes* [a Friesian section of *Coprinus* including the thin plicate species] lamellae thin, adnate, at first ascendant, not deliquescent ; spores brown or blackish brown with germ pore ; covering of the pileus and stipe and the edge of the lamellae with large erect hairs with thin walls ; cystidia on the sides of the lamellae none ». Kühner.

Development of the carpophores : Hemiangiocarpous (a complete study has been made by Kühner, *l. c.*).

Area : Almost cosmopolitan.

Limits : Kühner emphasizes the plicate and split surface of the pileus, the coprinoid structure of the hymenium, and the shape of the basidia which are characterized by a cylindric upper portion (similar to what is here called the « false Urnigera type ») as differences separating this genus from *Psathyrella* and making it comparable

with *Coprinus* On the other hand, he agrees with Buller that *Pseudocoprinus disseminatus* is not a typical *Coprinus.* The manner of formation of the hymenial ornamentation by folding always ends up in lamellae with non parallel sides in the adult specimens whereas the formation of the lamellae called coprinoid eventually produces lamellae with parallel sides. Romagnesi has recently accepted Kühner's new genus (1936) only to abandon it in a later paper (1941) on the grounds that it is not very different from *Coprinus* except for the non-deliquescent lamellae. He does not mention the development of the hymenophore, and it must be assumed that he is not in the possession of facts invalidating Buller's and Kühner's results. The author is therefore inclined to maintain the genus *Pseudocoprinus.*

State of knowledge : The type species is completely known in every aspect. There are, however, possibly other species which have not been studied completely up to this date, at least as far as the development of the lamellae is concerned.

Practical importance : None, unless in tropical deterioration of fabrics.

SPECIES

P. disseminatus (Pers. ex Fr.) Kühner (Psathyrella, Quel. ; Coprinus, S. F. Gray); probably also *P. crenatus* (Lasch) Kühner ex Romagnesi (Psathyrella, Quel. ; Coprinus, Ricken).

98. **MACROMETRULA** Donk & Sing., apud Singer

Mycologia **40** : 264, 1948.

Type species *Agaricus* (*Chitonia*) *rubriceps* Mass.

Characters : Habit of the carpophores somewhat like that of a *Volvariella* (pluteoid but volvate), with the lamellae not quite free but adnexed as in *Psathyrella ;* pileus with a distinct cellular epicutis as usual in *Psathyrella*, the isodiametric elements densely packed, somewhat smaller in the lower layer and there somewhat brownish in KOH ; basidia of the normal size as found in *Psathyrella,* 4 spored ; cystidia ventricose below and somewhat narrowed or capitate above (*Hydrophilum* type) ; also occasional echinulate bodies seen ; spores small, with broad and flattened germ pore, light umber in KOH, strongly discolored by H_2SO_4, with smooth complex wall, the

thick ; trama of the lamellae subregular, consisting of light brownish, subparallel hyphae when revived in KOH ; neither the trama nor any part of the spore wall pseudoamyloid or amyloid ; subhymenium very dense, of small elements ; stipe central, hollow, exanunlate but with a strongly developed cup-shaped membranous volva at the base with the free limb not attached to the surface of the stipe ; context white, consisting of hyphae with clamp connections. On soil in greenhouses.

Development of the carpophores : Probably hemiangiocarpous.

Area : The distribution of this genus is obscure since the only species known occurs in the Aroid house in Kew, England, and had obviously been introduced to Europe with some aroids

Limits : This genus is clearly distinct from *Psathyrella* which never has a well developed volva. The presence of a volva is in all other cases considered as a generic character (*Amanita, Volvariella, Clarkeinda*), and there is no reason why it should not be the main differentiating character in this case ; at least under the presumption that no intermediates exist, the hiatus between the two genera is sufficiently large.

State of knowledge : A small fragment of the edge of the lamellae which was taken from the type specimen at Kew was studied by Donk and Singer at the Farlow Herbarium ; later, more material was made available by the Director of the Kew Gardens, also from the type collection, clearly showing the presence of cystidia on the sides of the lamellae and the structure of the cuticle. This historical material in addition to the good picture published by Cooke, and Massee's original description, provide enough data on this fungus to insert it in the list of valid genera in the *Coprinaceae*.

Practical importance : None.

SPECIES

M. rubriceps (Mass.) Donk & Sing. (Agaricus, Mass. ; Chitonia, Mass.).

99. PSATHYRELLA (Fr.) Quél.

Champ. Jura Vosg., p. 178, 1872-73, em. Kühner

Type species : P. gracilis (Fr.) Quél.

Syn. : Agaricus subgenus *Psathyrella* Fr., *Epicrisis* p. 237, 1838
Psathyra (Fr.) Quél., *l. c.*, p. 148, non Spreng. (1818).
Hypholoma (Fr.) Quél., *l. c.*, p. 112, also sensu Romagnesi (1936).

Pannucia Karst., *Bidr. Finl. Nat. Folk* **32**: xxvi. 1879.
Drosophila Quél., *Enchiridion*, p. 115. 1886.
Lacrymaria Pat., *Hymen. Europ.*, p. 122. 1887.
Astylospora Fayod, *Ann. Sc. Nat., Bot.* VII **9**: 376. 1889.
Glyptospora Fayod, *l. c.*, p. 377.
Psilocybe Fayod, l. c., p. 377.
Cortiniopsis Schröter in Cohn, *Cryptog.-fl. Schles., Pilze*, p. 566. 1889.
Gymnochilus Clements, *Bot. Surv. Nebr.* **4**: 23. 1896, non Blume.
Hypholomopsis Earle, *Bull. N. Y. Bot. Gard.* **5**: 436. 1909.

Characters: Pileus campanulate, conical, or bullaceous at first, usually distinctly hygrophanous, often glittery when dry, with a distinct cellular epicutis, which is rarely covered partly by a fibrillose velar layer; lamellae narrowly adnexed (not free) to adnate, rarely adnato decurrent; hymenophoral trama regular to subregular, pigmented or hyaline in NH_4OH; basidia normal (larger than in *Agaricus*, even comparatively i. e. in relation with the spore size), sometimes 2 spored; cystidia present but often confined to the edges (cheilocystidia); hymenium not coprinoid (basidia often touching each other, the pseudoparaphyses not regularly interrupting them); the lamellae wedge shaped, of the inaequihymeniiferous type; spores in mass purplish fuscous to deep fuscous (« Java brown » to « Hindu » Maerz & Paul) to black, more rarely a dull reddish or russet, e. gr. « deep brownish vinaceous » (Ridgway), transparent or opaque under the microscope, with germ pore, smooth and without any kind of ornamentation but sometimes with a slightly rhomboid shape or subangular-tetraedric (at least appearing so in frontal view), small (below 6 µ) to large (to 20 µ) with complex wall; stipe centrally attached, usually strictly tubulose, flexuous or straight, with or without a veil which is sometimes annulate but usually not leaving a strong trace on the stipe, always devoid of a cup-shaped volva; pseudorrhiza and short rhizomorphs (white) sometimes present; context white or somewhat colored; hyphae usually with clamp connections. On the earth in and outside the woods, also on dead or living wood, also on dung, on living agarics and other *Basidiomycetes* (parasitically), and various other dead or living vegetable matter.

Development of the carpophores: Probably always hemiangiocarpous (known to be so in *P. epimyces*).

Area: Cosmopolitan.

Limits: This genus was originally considered as exclusively black spored. However, Quélet and Romagnesi (under the generic name *Drosophila*), and Kühner (under the name accepted here), and Lange

and Singer (under the name *Psathyra*) have emended the genus including several other genera or parts of them (*Psathyra, Hypholoma*, a large part of *Psilocybe* and some species of *Stropharia* and *Entoloma*) whereby a genus with a large number of sections, and species resulted. This emended genus *Psathyrella* is a very natural unit. It has been understood in about the same outline by the authors named above, yet, there are minor discrepancies which concern the following groups: *Lacrimaria* Pat., and *Hypholoma* sensu str. Romagnesi non al.

Lacrimaria Pat. has been admitted as a genus by all authors mentioned above, but after a discussion of the matter between the North American specialist of this genus, A. H. Smith, and the author, and after further comparison of representative specimens, the genus *Lacrimaria* does not appear to be well founded. The roughness of the outer spore wall has several times been found to be a character of specific rather than generic value. Otherwise, the species of *Lacrimaria* are not clearly separable from the species of that part of *Psathyrella* called *Hypholoma* sensu str. (not section) by Romagnesi (non al.). Since the name *Hypholoma* has been preoccupied by Romagnesi himself for a section different from the *Lacrimaria* group, *Lacrimaria* plus *Hypholoma* Romagnesi have been reunited here under the subgeneric name *Lacrimaria*. This emended concept of *Lacrimaria* is still not an autonomous genus. The author agrees with Kühner (1936) who stated his belief in the generic identity of *Hypholoma* sensu str. Romagnesi and *Psathyrella*.

As far as the separation of *Psathyrella* from *Macrometrula* and *Pseudocoprinus* are concerned, see under the corresponding paragraphs in the latter two genera.

State of knowledge: The genus *Psathyrella* or its nomenclatorial equivalents, or even its original parts as used in the Saccardo scheme, have not until very recently attracted the attention of modern mycologists. However, Romagnesi in France, and A. H. Smith in the United States have recently interested themselves in the sectional taxonomy (Romagnesi) and the definition of various species (Smith) in this vast group but neither has yet had time to even begin monographic work. The temperate flora contains several dozens of good species — few of them fully known at present — while the author admits only 25 species from all over the world in order to make sure that they are inserted correctly and not in duplication of older names.

The classification adopted below is as close as possible to that proposed by Romagnesi, yet taking into account several facts which

call for slight alterations in Romagnesi's scheme, and also changing several names because of a stricter application of the nomenclatorial rules.

Practical importance : P. Candolleana is an excellent edible fungus but little used. It is better known in North America (under the name *Hypholoma incertum*) than in Europe.

SPECIES

Subgenus I. **Lacrimaria** (Pat.) Sm. & Sing. (*Lacrymaria* Pat. 1887 ut genus). A fibrillose innate layer of colored hyphae forming the continuation of the veil on the surface of the pileus partly covers the (sometimes less distinct) cellular epithelium ; spores sometimes rough or warty.

Type species : P. velutina (Pers. ex Fr.) Sing.

P. velutina (Pers. ex Fr.) Sing. (Hypholoma, Quel — this is called Hypholoma, Lacrymaria, etc., lacrimabunda by many authors, but incorrectly so); *P. scobinacea* (Fr.) Sing. (Stropharia, Sacc. ; Hypholoma, Ricken) and species closely related to the latter (such as *Hypholoma lepidotum* Bres. ; *Atylospora Weberi* Murr. ; *Hypholoma silvestre* Gillet ; *Agaricus lacrimabundus* Fr. sensu Konr. & Maubl. which may be the same as *Stropharia cotonea* Quél.), and other smooth-spored species.

Subgenus II. **Hypholoma** (Fr.) Romagnesi (1944) (*Hypholoma* (Fr.) Quél. ut genus non sensu Romagnesi 1936). Pleurocystidia present, utriform (ventricose capitate), or absent and then the cheilocystidia utriform, or at least slightly narrowed in the middle and broadly capitate, or broadly ampullaceous with the neck broader than half the diameter of the ventricose part beneath ; veil appendiculate.

Type species : P. Candolleana (Fr.) A. H. Smith.

Sect. 1. FRAGILISSIMAE Romagnesi (1944). Trama of the lamellae hyaline, entire trama very little pigmented if at all, at least the larger portion of it completely hyaline ; cystidia on the sides of the lamellae none ; spores larger than 10 µ.

Type species : P. marcescibilis (Britz.) Sing.

P. marcescibilis (Britz.) Sing. (Hypholoma, Sacc. ; Drosophila, Romagnesi ; Psathyra fragilissima Lange), and probably several more species.

Section 2. CANDOLLEANAE Romagnesi (1944). Trama of the

lamellae hyaline; cystidia on the sides of the lamellae none; spores smaller than 10 µ.

Type species : P. Candolleana (Fr.) A. H. Smith.

P. Candolleana (Fr.) A. H. Smith, with forma *incerta* (Peck) and f. *coriaria* (Pan.) Sing. [Hypholoma Candolleanum (Fr.) Quél.; Drosophila, Quél ; Hypholoma incertum (Peck) Sacc.; Hypholoma coriarium Panazzi; forms of *P. Candolleana* are also often referred to under the name Hypholoma appendiculatum but the latter is a species of doubtful standing].

Note : The section *Sphintrigeri* may be transferred here from *Stropharia* and inserted as an additional section. The author has not re-studied the species involved, and consequently omits this group here. *Psathyrella epimyces* (Peck) A. H. Smith (Panaeolus, Peck; Stropharia, Atk.) is intermediate between the *Sphintrigeri* and *Candolleanae*.

Sect. 3. **FATUAE** Romagnesi (1944). Trama of the lamellae hyaline; cystidia on the sides of the lamellae present; spores rather small (smaller than 11 µ); carpophores in most species rather large.

Type species : P. pygmaea (Quel.) Sing.

P. pygmaea (Quél.) Sing. (Drosophila, Quel. ; Psathyrella consimilis Bres. & Henn.; Hypholoma minutellum Hoehnel ; Psathyra gyroflexa (Fr.) Quél. sensu R. Maire non al. — synonymy according to data published by Romagnesi); *P. casca* (Fr.) Sing. (sensu Romagnesi) (Hypholoma, Quél. ; *P. spadiceogrisea* (Schaeff. ex Fr.) A. H. Smith (Psathyra, Quel. ; Drosophila, Quél. ; Psilocybe, Boudier), at least in the sense of Ricken, Lange and Romagnesi.

Sect. 4. **TYPHICOLAE** Romagnesi (1944). Hymenophoral trama colored with membrana pigment; spores larger than 10 µ; cystidia on the sides of the lamellae none; carpophores small or rather small; lamellae rather narrowly adnexed.

Type species : P. Typhae (Kalchbr.) Sing.

P. Typhae (Kalchbr.) Sing. (Psathyra, Sacc.; Drosophila, Romagnesi) and probably many other species.

Sect. 5. **HYDROPHILAE** Romagnesi (1944), em. Trama of the lamellae colored with a membrana pigment; spores small (up to 6.5 µ long.); cystidia absent on the sides of the lamellae, or more rarely present on both the edges and the sides of the lamellae; carpophores rather large (i. e. size of those of *P. Candolleana* or slightly smaller); spores under the microscope not very deeply colored.

Type species : P. hydrophila (Bull. ex Fr.) Sing.

P. hydrophila (Bull. ex Fr.) Sing. (Hypholoma, Quél.; Psathyra, Bertrand; Psilocybe, Gillet; Drosophila, Quél.).

Sect. 6. **FRUSTULENTAE** Romagnesi (1944 ut subsect. sectionis *Hydrophilarum*). Differing from section 5 in the spores measuring from 6-11.5 μ in length, and in the constant presence of numerous pleurocystidia, also in smaller size and habit (comparable with that of *P. gracilis*), and very fugacious and slight veil.

Type species: P. frustulenta (Fr.) A. H. Smith.

P. frustulenta (Fr.) A. H. Smith sensu A. H. Smith non Ricken (Psathyra, Sacc.; Drosophila, Romagnesi).

Subgenus III. **Homophron** Britz. (1883 ut subgenus *Agarici*) [*Drosophila*, subgenus *Psathyra* (Fr.) Romagnesi (sensu Romagnesi non Fries)][114].

Cystidia on the sides of the lamellae not utriform, with narrow, thick walled (to solid) apex which is strongly, more rarely slightly muricate (incrusted with crystals), refringent and sometimes somewhat colored (thus showing all characteristics of metuloids); margin of the pileus often involute, without any veil; pileus fleshy and comparatively thick; stipe often fasciculate and lignicolous; spores dark colored, or more often rather light colored, even as bright as «deep brownish vinaceous» (Ridgway).

Type species: P. spadicea (Schaeff. ex Fr.) Sing.

P. spadicea (Schaeff. ex Fr.) Sing. (Psilocybe, Quél.; Drosophila, Quél.); *P. olympiana* A. H. Smith; *P. sarcocephala* (Fr.) Sing. (Psilocybe, Gillet; Psathyra, Bertrand); *P. subcernua* (Schulzer) Sing. [Agaricus (Nolanea) subcernuus) Schulzer; Psathyra, Hoehnel; Chitopilus comissans Peck; Psilocybe comissans (Peck) Peck 1908.

Subgenus IV. **Pannucia** (Karst.) Romagnesi (1944) (Genus Pannucia Karst. 1879). Cystidia never utriform, rather ampullaceous or fusiform, with apical portion less than half as thick as the broadest portion of the cystidium, neither thick walled nor muricate, rarely with very slightly and rather evenly thickened wall which is sometimes beset with some crystals, but then the margin of the pileus always distinctly veiled in young carpophores; spores always small (i. e. smaller than 10 μ).

[114] *P. spadicea* is the species on which this subgenus is mainly based; it was considered as *Psilocybe* by Fries. Consequently it is not recommended to use the subgeneric name *Psathyra* in this sense. In fact, it appears impossible, and also unnecessary since *Homophron* was used by Britzelmayr mainly for this group since 1883.

Type species : P. noli tangere (Fr.) Sing.[115].

P. noli tangere (Fr.) Sing. (Pannucia, Karst.; Psathyra, Quél.); *P. pennata* (Fr.) Sing. (sensu Ricken) and *P. pennata* (Fr.) Sing. (sensu Lange)[116]: *P. gossypina* (Bull. ex Fr.) Sing. (Psathyra, Quél.; Drosophila, Quél.); *P. fibrillosa* (Pers. ex Fr.) Sing. (sensu Ricken) (Psathyra, Quél.; Drosophila, Quél.), and several other species.

Subgenus V. **Eupsathyrella** Sing. [*Drosophila* subgenus *Psathyrella* (Fr.) Romagnesi 1944]. Distinguished from the preceding subgenus mainly in the large spores which are practically black in print in most of the species, or at least blackish fuscous.

Type species : P. gracilis (Fr.) Quél.

P. gracilis (Fr.) Quel.

Sect. 7. **GRACILES** Romagnesi (1944). Hymenophoral trama hyaline; stipe with a more or less distinct pseudorrhiza.

Type species. As in the genus and subgenus.

Sect. 8. **MICRORHIZAE** Romagnesi (1944). Trama with a membrana pigment and consequently slightly to strongly colored; stipe with a pseudorrhiza.

Type species : P. microrhiza (Lasch) Sing.

P. microrhiza (Lasch) Sing. (Psathyra, Sacc.; Drosophila, Romagnesi).

Sect. 9. **ATOMATAE** Romagnesi (1944). Hymenophoral trama as in the preceding section; stipe without pseudorrhiza; veil usually present but fugacious; pleurocystidia usually present but scattered; pileus up to 20 mm broad.

Type species : P. prona (Fr.) Gillet sensu Ricken.

P. prona (Fr.) Gillet sensu Ricken (Coprinarius, Quél.); perhaps also *P. atomata* (Fr.) Quél.

Sect. 10. **SUBATRATAE** Romagnesi (1944). Trama as in section 2; pseudorrhiza absent; veil absolutely none, allegedly even in

[115] Romagnesi separates two sections within this rather homogeneous group. There is a question whether or not such a separation is justified, and much seems to indicate that the subgenus should perhaps rather remain unsubdivided. However, even if the sections were accepted, the position of the type species of the subgenus is unknown since not all the data required by Romagnesi for the determination of the section are known in *P. noli-tangere*. Consequently, there was no choice but to omit the sections at present.

[116] One of the interpretations will eventually have to be renamed unless an older name can be found for the species believed to be not the Friesian conception.

the primordia (at least macroscopically); pleurocystidia none; spores usually very large (12-18 µ); pileus often broader than 20 mm.

Type species: *P. subatrata* (Batsch ex Fr.) Gillet.

P. subatrata (Batsch ex Fr.) Gillet (Drosophila, Quél.).

Subgenus VI. **Conocybella** A. H. Smith in litt. ex Sing. (1948). Much like subgenus IV but the cheilocystidia of the *Conocybe* type i. e. broadly ventricose below with a small globose stalked capitellum at the apex or vesiculose; pleurocystidia none; spores small (smaller than 10 µ).

Type species: *P. michiganensis* A. H. Smith.

P. michiganensis A. H. Smith; probably also *P. Roystoniae* (Earle) Sing. (*Gymnochilus*, Earle; *Hypholoma*, Sacc.).

Subfamily **Panaeoloideae** Sing.

Ann. Mycol. **34**: 339. 1936.

Type genus: *Panaeolus* (Fr.) Quél.

Syn.: *Panaeoleae* Romagnesi, *Rev. Mycol.* **2**: 23. 1937 (nom. nud.) (ut tribus *Scolosporacearum*).
Panaeolés Kühner *Bull. Soc. Mycol. Fr.* **52**: 33. 1936 (ut série).

Characters: Pileus with cellular epicutis; lamellae not deliquescent, becoming very unequally dusted with the spores when mature, and consequently rather spotty when seen from the sides, but belonging to the aequihymeniiferous type, so-called *Panaeolus* subtype (Buller); spores often lemon-shaped, not discolored when treated with concentrated H_2SO_4; habit characteriscally campanulate and rarely expanding, more rarely semiglobose and not expanding.

KEY TO THE GENERA

A. Cystidia absent on the sides of the lamellae.
  B. Spore print deep purplish fuscous; spores warty . . . 100. *Panaeolina*
  B. Spore print black; spores smooth. . . . 101. *Panaeolus*
A. Cystidia present on the sides of the lamellae
  C. Cystidia of the metuloid type: colored, thick-walled, acute; habit of the carpophores exactly as in *Panaeolus*. Predominantly tropical genus. . . . 102. *Copelandia*
  C. Cystidia similar to the chrysocystidia, with refringent inclosure which is, however, not distinctly yellow in ammonia, with hyaline, thin wall and with broadly rounded apex; habit of the carpophores different from that of the typical Panaeoli, more fleshy and thick, never hygrophanous; stipe

100. PANAEOLINA R. Maire

Publ. Junta Cienc. Nat. Barcelona 1933, p. 109. 1933

Type species : *P. foenisecii* (Pers. ex Fr.) R. Maire.

Syn. : *Psilocybe* Fayod, *Ann. Sc. Nat., Bot.* VII **9** : 377. 1889, non al.

Characters : Those of the subfamily ; spores deep purplish fuscous in print, verrucose or verruculose under the microscope. On the ground in open places.

Development of the carpophores : Unknown.

Area : Circumpolar ; perhaps also in the southern hemisphere.

Limits : This genus has been confused with *Psilocybe* in the past, and Kühner (1929) and Maire (1933) separated it from *Psilocybe*. Some authors proposed to combine it with *Panaeolus*. In the author's opinion, this is a very good genus, and will be kept separate from *Panaeolus* as long as no intermediate species can be discovered.

State of knowledge : Only one well known species enters *Panaeolina* at present, — the type species.

SPECIES

P. foenisecii (Pers. ex Fr.) R. Maire (Psilocybe, Quél ; Drosophila, Quél. ; Panaeolus, Kühner).

101. PANAEOLUS (Fr.) Quél.

Champ. Jura. Vosg. p. 151. 1872-73

Type species : *P. campanulatus* (L. ex Fr.) Quél.

Syn. : *Chalymmota* Karst., *Hattsv., Bidr. Finl. Nat. Folk* **32** : xxvii. 1879
Coprinarius Quél., *Enchiridion*, p. 118. 1886.

Characters : Pileus campanulate, more rarely conical, usually pigmented, rarely without pigment at first, not or little expanding in age, often more or less hygrophanous, appendiculate with a white or whitish, eventually black stained veil, or naked, viscid or dry ; epicutis cellular ; lamellae strongly variegated because of the basidia maturing in patches (« *Panaeolus*-subtype »), ascendant at least in youth ; cheilocystidia present ; other kinds of cystidia absent ; spores lemon-shaped, rarely more evenly ellipsoid, smooth, black in mass and almost so (not transparent) under the microscope, opaque,

rather large (larger than 10 µ in all species known), with distinct broad germ pore, with thick, complex wall; stipe usually strongly elongated in comparison with the diameter of the pileus, rather thin, usually at least partly pigmented, tubulose, central. On the soil and on dung.

Development of the carpophores : Probably hemiangiocarpous, at least in most species, and known to be so in *P. sphinctrinus.*

Area : Cosmopolitan.

Limits : Some authors are inclined to combine all elements of the *Panaeoloideae* into this one genus. Considering the sharpness of the characters emphasized here, the strong hiatus between these genera, and the comparative value of the genera in neighboring groups, the author is firmly convinced that these units are perfectly good autonomous genera, and *Panaeolus* should be understood in the emended, i. e. restricted interpretation, excluding *Panaeolina, Anellaria* and *Copelandia.*

State of knowledge : The species belonging in *Panaeolus* have all been studied thoroughly but their separation is still difficult in many cases. One is often tempted to doubt the value of the characters supposedly distinctive as introduced by Fries. The degree of hygrophanity of the pileus and the presence or absence of the appendiculation on the margin do not seem to be as constant as Fries believed they were. It must be hoped that a future monograph will bring more light regarding the delimitation of the species within *Panaeolus.* Six species are here admitted.

Practical importance : Panaeolus sphinctrinus and *P. papilionaceus* are used as intoxicating drugs in Central America by certain Indian populations, together with *Psilocybe cubensis.* In large doses (i. e. 50 60 specimens) they are poisonous. *Panaeolus* occasionally appears as a weed fungus in mushroom beds, but the damage inflicted is probably negligible.

SPECIES

P. sphinctrinus (Fr.) Quel. [P. campanulatus (L. ex Fr.) Quél. non Agaricus campanulatus Bull. ex Fr. 1821 ; P. Linnaeanus Imai] ; *P. acuminatus* (Schaeff. ex Fr.) Quél. ; *P. retirugis* (Fr.) Quél. ; *P. papilionaceus* (Bull. p p. ex Fr. p. p. em. Fr. 1838) Quél. ; *P. guttulatus* Bres. ; *P. subbalteatus* (Berk. & Br.) Sacc. ; probably also *P. fimicola* (Fr.) Gillet and *P fimiputris* (Bull. ex Fr.) Quél. (Anellaria, Karst.).

KEY TO THE SPECIES

All keys published thus far will serve the purpose of determining the species according to the Friesian conceptions; this goes for both Europe and North America as well as temperate Asia since the species occurring in the northern hemisphere are probably not very different in these continents

102. COPELANDIA Bres.

Hedwigia 53. 51. 1913.

Type species: *Copelandia papilionacea* (Bull. ex Fr.) Bres. sensu Bres., non *Panaeolus papilionaceus* (Bull. ex Fr.) Quél.

Characters: Pileus and stipe pigmented; pileus fleshy or almost membranous, with cellular epicutis; lamellae variegated; hymenophoral trama regular; metuloids melleous with thick walls and subacute narrowly mucronate apex which is sometimes solid; spore print black; spores smooth, lemon shaped, opaque, with complex wall and broad, distinct germ pore; stipe central, thin, rather fragile; context often changing color (bluing, etc.). On soil and on dung.

Development of the carpophores: Unknown.

Area: In warmer climates, Florida, Central America and west to the Philippines and Dutch East Indies.

Limits: The genus *Copelandia* differs from *Panaeolus* not merely in the presence of cystidia at the edge and on the sides of the lamellae instead of merely on the edge, — but also by the peculiar character of the cystidia occurring on the edges, and by the discoloration of the context which is reminiscent of that in *Psilocybe* sect. *Cyanescentes*.

State of knowledge: The only species known to belong in *Copelandia* is reasonably well known. It may be expected that fresh specimens will reveal certain chemical characters to be added to those indicated above.

Practical importance: Unknown.

SPECIES

C. cyanescens (Berk. & Br.) Sing. (Panaeolus, Sacc.; Copelandia « papilionacea » (Bull.) Bres. non Agaricus papilionaceus sensu Fries 1838; Panaeolus Westii Murr.; Copelandia, Sing. 1944).

103. ANELLARIA Karst.

Hattsv., Bidr. Finl. Nat. Folk **32**: xxvii. 1879, em

Type species. *A. separata* (L. ex Fr.) Karst.

Characters: Pileus comparatively fleshy (much more so than in *Panaeolus*), with very little pigment (practically white in most specimens, or with a slight ochraceous hue on the disc), viscid, with wide sterile projecting margin, campanulate, slightly expanding but not flattening in age, with well developed epithelium; lamellae variegated as in *Panaeolus*; hymenophoral trama regular but its elements not all truly parallel and not equal in size, some of them rather short; basidia normally clavate, 4 spored; cheilocystidia versiform; cystidioles of the sides of the lamellae very voluminous, vesiculose, some strongly suggesting the chrysocystidia of the *Strophariaceae* but not distinctly yellow in ammonia and not distinctly bluing in cresyl blue, strictly hyaline; spore print black; spores under the microscope deep purplish fuscous to black, opaque, smooth, always very large, with complex wall and broad distinct germ pore, not discolored in H_2SO_4, ellipsoid to lemon shaped; stipe with traces of a veil but part or all of it often found on the fringe of the margin, either solid, or annulate, or both, rather fleshy, practically not pigmented, central, rather long, sometimes viscid; context white and unchanging, fleshy, consisting of hyphae with clamp connections. On dung and on manured soil.

Development of the carpophores: Probably always hemiangiocarpous.

Area: Cosmopolitan, one species in North America north to Michigan, otherwise nearly pantropical and subtropical; the other more boreal and montane.

Limits: The practical absence of coloring matter, combined with the gelatinosity of certain surface layers of the carpophores, the fleshy pileus and stipe, and the solid, annulate stipe are enough characters to define this genus macroscopically, even if it were not characterized by a simple, and dependable microscopical feature, the pleurocystidia.

State of knowledge: Two species are known and all necessary data about them are available.

Practical importance: Both species are edible.

SPECIES

A. semiovata (Sow. ex Fr.) Pearson & Dennis [Panaeolus, Lundell & Nannfeldt; Panaeolus separatus (L. ex Fr.) Quél.; Anellaria, Karst.]; *A. sepulchralis* (Berk. [117]) Sing. [Panaeolus, Sacc.; Panaeolus solidipes (Peck) Sacc.].

KEY TO THE SPECIES

A. Annulus well developed. Northern and subalpine species (in the mountains up to 3000 m.), circumpolar and mountains of South America. *A. semiovata*

A. Annulus none or poorly developed. From Celebes through Oceania east to Central America and the West Indies, and in this continent north to Michigan, south to Argentina. *A. sepulchralis*

BOLBITIACEAE Sing.

Pap. Mich. Acad. Sc., Arts, Lett. **32**: 147. 1946 (publ. 1948)

Type genus: Bolbitius Fr.

Characters: Hymenophore lamellate to venose or with oblique anastomoses forming chambers (loculi); epicutis often consisting of elongate repent, parallel elements; but in the fleshy forms, epicutis always consisting of piriform (erect) or globose cells, and then the pileus usually hygrophanous and often glistening when dry; dermatocystidia differentiated from the elements of the epicutis, or not; cystidia present only on the edges (cheilocystidia), or also on the sides of the lamellae; spore print a very rich, deep but bright rusty color, more rarely rusty fuscous or sordid brown (i.e. approaching the color of the spore print of the Inocybes), never in the colors indicated for the *Coprinaceae*, and never pink, ochraceous, or green; spores melleous to rusty under the microscope, smooth, very rarely rough or verrucose, always with a germ pore (Pl. XIII, 1) but in certain species the germ pore not very distinct, and in this case it may be thought to be absent (*Agrocybe erebia* and related species, etc.); ba

[117] The description of the type is not fully in accordance with the characters of this species, yet, authentic material from the Curtis Herbarium is undoubtedly the same as *Panaeolus solidipes* and antedates this latter considerably. It must be assumed that the original type was in poor condition for a macroscopical description when received by Berkeley, or else was not accompanied by notes, or by poor ones. This condition is rather frequent as far as tropical species are concerned.

sidia comparatively short and broad, 1, 2, 3, or 4 spored, two-spored races common; stipe fleshy to fragile, always central, often with dermatocystidia; clamp connections always present in normal, i. e. heterothallic forms (but parthenogenetic and homothallic forms of the same species often clampless); growing on wood and on humus in the woods, on earth, on various vegetable matter, or on dung in and outside the woods, also on sawdust, or charcoal, frequently found on lawns, in gardens, in greenhouses, etc.

Limits: As for the most important, central group of genera, i. e. *Bolbitius*, *Conocybe*, *Galerella*, and *Pholiotina*, there is no need of additional delimitation since these genera, as a whole are abundantly different from all other agarics, yet clearly intermediate between the *Coprinaceae* and the *Strophariaceae*.

However, certain problems arise when such peripheric genera as *Cyttarophyllum* at one extreme end of the family, and *Agrocybe* at the other end, are contemplated.

(1) *Cyttarophyllum:* This genus was first described by Heim as a subgenus of *Conocybe*, an arrangement which does not sufficiently express the differences between *Cyttarophyllum* and *Conocybe* which are very considerable, but on the other hand shows that the affinity between the central group of the *Bolbitiaceae* and *Cyttarophyllum* is close enough to justify their combination into one single family. In fact, the color, structure and size of the spores is so much the same in *Cyttarophyllum* and in the remaining genera of the *Bolbitiaceae* that they cannot be distinguished if seen isolated from the carpophores. Even the shape of the carpophores is not unusual in the genus *Conocybe*, and a somewhat marasmioid stipe is found in the subgenus *Ochromarasmius* of the latter genus. What really differs is the non-cellular epicutis and the development of the hymenophore in *Cyttarophyllum*. In that regard, *Cyttarophyllum* is just one step closer to the *Gastromycetes* of the *Secotiaceae* type, and it is now known precisely which *Gastromycetes*: The genus *Galeropsis* as described by Velenovsky & Dvořak and restudied by Singer (1936). *Galeropsis* is, in habit, consistency and structure so similar to *Cyttarophyllum*, it may be asked whether it would not be preferable to separate *Cyttarophyllum* from the *Bolbitiaceae* and transfer them to the *Secotiaceae*. The author disagrees with this point of view. Even if the mechanism of separation of the margin of the pileus from the stipe is different in *Cyttarophyllum* and probably delayed as compared with *Conocybe*, the presence of cheilocystidia in *Cyttarophyllum* shows

that the fungus in question has not a columella to which the hymenophore of the gleba is attached in the early stages but that the prolongation of the stipe above the margin of the pileus is a true apical portion of a stipe which is free from the tissue of the latter. Under these circumstances it would be difficult to speak of *Cyttarophyllum* as of a Gastromycete, even theoretically.

If then *Cyttarophyllum* is to remain among the *Agaricales*, there is no better place for it in the system than at the fringes of the *Bolbitiaceae*. One may consider it as a side branch adapted to xerophytic conditions (but why then the simplified structure of the cuticle?), or, in accordance with the opinion expressed by the author, as a link between the *Gastromycetes* and the *Agaricales*, representing a «halting place» in the evolutionary line leading from the *Gastromycetes* to the *Agaricales*.

(2) *Agrocybe*: This genus was once considered as belonging to a group of agarics now separated by Singer & Smith under the name *Strophariaceae*. This disposal of *Agrocybe* dates back to Van Overeem who published a nomen nudum (*Phaeodeconica*) with the intention to designate what is now called *Agrocybe* Fayod, and put both this and the genus *Stropharia* into a family (also a nomen nudum) which he called *Strophariaceae*. This latter name was later validated by Singer & Smith. Another disposal of *Agrocybe* can be found in Romagnesi's classification published at the occasion of the publication of his *Florule des Bois de la Grange*. Here the tribus *Agrocybeae* is one of the two tribus composing the family *Phaeolaceae* (another nomen nudum, and formed not according to the rules of nomenclature); the other tribus is the *Hebelomeae*. The *Hebelomeae* are a group of agarics which is here considered as belonging in the family *Cortinariaceae*. Summing up, we may therefore put the question at hand in the following words: Is *Agrocybe* closer to the *Cortinariaceae* (*Hebeloma*), or the *Strophariaceae* (*Stropharia*), or the *Bolbitiaceae* (*Bolbitius*)? Both Romagnesi's and Van Overeem's arrangement have in their favor a certain superficial similarity between the genera thus assembled. In fact, *Stropharia stercoraria* is often very similar to certain species of *Agrocybe* when seen in the field, and certain smaller species of *Hebeloma* may well suggest *Agrocybe* because of their color, slight viscidity, whitish stipe, and color of the lamellae. Nevertheless, if the color of the spores of *Agrocybe* is disregarded, one will notice that the microscopical characters are almost precisely identical in *Agrocybe* and in the central group of genera in the *Bolbitiaceae*.

If no spore print is available, one will hardly be always in a position to tell the spores of *Agrocybe* from those of the other genera of the *Bolbitiaceae*. Furthermore, the preferences of habitat as observed in the Agrocybes are much more like those of the *Conocybe* group than those of the *Cortinariaceae* which are mainly forest fungi, often forming mycorrhiza. And finally, a close observation of the spore prints and comparison with color charts will reveal that the colors observed in *Agrocybe* have a more rusty tone than those of either *Stropharia* or *Hebeloma*. This situation is even more clearly apparent when the fact is taken into consideration that in North America at least one species of *Bolbitius* — otherwise completely identical with the classical species of that genus as far as generic characters are concerned — has dull brown spore print instead of the rich rusty color usually observed in *Bolbitius*, *Conocybe*, *Pholiotina*, etc. This, in the author's opinion, is the final, decisive fact that proves that the group with a cellular epicutis on the pileus and a germ pore on the spores is an independent group that should not artificially be divided into families according to the shade of spore print color. It has been said that some species of *Agrocybe* have spores without germ pore. However, an attentive study of these spores with application of the proper technique will show that all species of *Agrocybe* have spores with germ pore, only in some of them the percentage of spores with entire wall is comparatively larger than in others, and in some species the germ pore is very small and the apex of the spore is not truncate enough to make the observation of the germ pore easy. A varying degree of development of the germ pore in a single spore print, and even more in a single hymenophore preparation is not uncommon. The presence of a limited number of spores with germ pore is usually considered as decisive for a positive statement on its presence in the species generally.

Consequently, *Agrocybe* is considered as another genus of the *Bolbitiaceae*.

KEY TO THE GENERA

A. Epicutis a cutis, i. e. consisting of repent elongate elements; context of the stipe rather dry and somewhat tough and at the same time rather light in weight; pileus globose or more often narrowly fusoid, higher than broad, with the margin appressed to the stipe (not incurved nor even perpendicular to the longitudinal axis of the stipe); the young stages similar in habit to *Galeropsis* and other *Secotiaceae* 104 ***Cyttarophyllum***

A. Epicutis consisting of an epithelium, or a layer of pear-shaped or stalked-

vesiculose short elements which form a hymeniform outer layer above a hypodermium of different structure ; context of the stipe rarely dry and toughish, usually fleshy but thin and fragile to, more rarely, thick and fleshy-soft, pileus rarely globose or fusoid, usually semi globose to campanulate or conical in youth, and frequently expanding in age, usually broader than high, when quite mature ; margin not appressed to the stipe ; habit never comparable with the *Secotiaceae*.

B. Spore print rusty brown.

C. Pileus viscid, plicate-sulcate as in some Coprini ; stipe white or whitish even near the base ; trama of the lamellae regular ; cheilocystidia not abruptly capitate. 109. *Bolbitius*

C. Fungi not combining these characters.

D. Lamellae very narrow, decurrent, triangular ; pileus expanded in age. 108. *Tubariopsis*

D. Lamellae not abnormally narrow and decurrent and triangular ; pileus expanding in age at least to a certain degree, or more rareley not expanding

E. Trama of the lamellae consisting of a very reduced mediostratum, the hymenopodia on both sides of it very strongly developed and almost touching each other ; veil mostly completely absent ; pileus plicate or cheilocystidia with a stalked globule at the apex (abruptly capitate)

F. Pileus plicate sulcate as in some *Coprini* ; cheilocystidia ampullaceous. 106. *Galerella*

F. Pileus subsulcate or transparently striate when moist, or even quite smooth ; cheilocystidia abruptly capitate 105. *Conocybe*

E. Trama of the lamellae normally regular (mediostratum well developed, many of its elements rather voluminous) ; veil present or absent ; pileus never plicate-sulcate ; cheilocystidia rarely capitate. 107. *Pholiotina*

B. Spore print ferruginous fuscous, or sordid brown.

G. Lamellae linear, narrow ; context of the pileus very thin ; margin sulcate. (see *Bolbitius*)

G. Lamellae broad to moderately narrow, not linear ; context of the pileus comparatively thick ; margin not sulcate 110. *Agrocybe*

104. CYTTAROPHYLLUM (Heim) Sing.,

Beih. Bot. Centralbl. **56** (Abt. B) : 147. 1936 ; *Ann. Mycol.* **34** : 344. 1936

Type species : Conocybe Besseyi (Peck) Heim, sensu Heim.

Syn. : Conocybe subgen. *Cyttarophyllum* Heim, *C. R. Acad. Fr.* **192** : 291. 1931.

Characters : Habit of the carpophores very characteristic because

acuminate pileus and the amplectant margin, i. e. the margin of the pileus is initially not incurved and not even directed against the surface of the stipe at an angle but is collariately attached to it and firmly appressed, later dissociating itself by a loosening up the coherence of the fibrils, i. e becoming more or less lacerate; hymenophore distinctly lamellately arranged but the lamellae frequently anastomosing by veins or by lamellate anastomoses (i. e. anastomoses of a breadth equalling that of the lamellae) causing a cyttaroid appearance; lamellae very narrow, strongly and permanently ascendant; spore print not obtained but massed spores on the hymenophore a rich rust color, becoming even richer colored in ammonia or melleous in the same medium according to the species, with distinct germ pore, smooth, with thick or moderately thick, complex wall, distinctly heterotropic (axillarly asymmetric), fusoid amygdaliform or more frequently ellipsoid; basidia characteristically ampullaceous or ventricose above and below and subconstricted in the middle (false *Crucigera* type), either 2 or 4 spored (mixed), or all 4 spored, with numerous pseudoparaphyses which are vesiculose, without true cystidia on the sides of the lamellae but with numerous (but not crowded) cheilocystidia along the edge of the lamellae which is free from the stipe; hyphae of the epicutis of the pileus and the cortical layer of the stipe parallel with each other, strictly repent, filamentous but moderately thin and either thin walled or with moderately thick walls; veil often present, cortinoid, pallid but not ordinarily well developed; context rather light in weight and tenacious in the manner of the *Secotiaceae* rather than in the manner of the *Polyporaceae*, not as fleshy as in other genera of the *Bolbitiaceae*; hyphae with clamp connections. Mostly outside the wood in xerophytic associations (deserts, steppes, dry mountain sides, etc.), on the ground or on herbaceous fragments.

Development of the carpophores. Probably nearly angiocarpous (very early stages have not been studied by the author).

Area. Widespread in drier climates: Western North America, South Africa, probably also in the cold dry zone of South America.

Limits: The separation of *Cyttarophyllum* from *Conocybe* does not cause any difficulties. The separation from *Galeropsis* is more difficult since the latter looks much more like *Cyttarophyllum*, and Singer (1936) and Zeller (1943) did not correctly differentiate between these genera. The author has not found any cheilocystidia in *Galeropsis*, the spores are less asymmetric in the latter genus, and the sterig-

mata more filamentous, upright and somewhat undulate, rather than typically half-sickle-shaped as in most agarics. The inner (pointing toward the columella) edges of the tramal plates are more obtuse in *Galeropsis* than in *Cyttarophyllum* where the lamellae are much more typically agaricoid. Though the specimens studied by the author were all mature, the obtuse edge of the lamellae would indicate a different development of the carpophores and especially the hymenophores than that of *Cyttarophyllum*.

Nevertheless, there cannot be the slightest doubt but that *Cyttarophyllum* and *Galeropsis* are most closely related to each other. It is only for the sake of keeping within the subject of the present book that the *Secotiaceae* are not treated here. *Galeropsis* is the one genus among the *Secotiaceae* most closely related to the *Bolbitiaceae*. But other *Gastromycetes* still show many characters reminiscent of this same group. A monograph of *Secotium* would bring this out, since there are about three different groups of species with very distinct spore characters in that genus, a fact that has not been emphasized in the literature on *Gastromycetes*.

State of knowledge: The four species composing this genus are well known.

Practical importance: None.

SPECIES

C. polytrichoides (Zeller) Sing. (Secotium, Zeller; Galeropsis, Zeller 1943); *C. cucullatum* (Shope & Seaver) Sing. (Bolbitius, & Seaver, Galeropsis, Sing.; Secotium longipes Zeller); *C. liberatum* (Kalchbrenner apud Thuemen) Sing. (Bolbitius, Kalchbr.); *C. Besseyi* (Peck) Sing. (Galera, Peck; Conocybe, Heim).

KEY TO THE SPECIES

A. Pileus globose or ovoid; cheilocystidia ampullaceous or subulate or subventricose below, with capitate apex; lamellae strongly anastomosing with ridges of nearly equal height with the radiating lamellae. North America; according to Heim also in Madagascar [44]. *C. Besseyi*

[44] The specific identity of two rare species divided from each other geographically by such enormous areas of land and ocean, and growing under climatically so very different conditions, is very puzzling. Possibly, a further study of the two types, will make it possible to separate these forms specifically

A. Pileus narrowly fusoid or subcylindric with acute tip or apical appendage; cheilocystidia as described above, or of different shape; lamellae mostly less strongly anastomosing.

B. Spores rusty-melleous as in *Agrocybe* when seen under the microscope in ammoniacal medium

C. Spores ellipsoid-amygdaloid, 6.8-7.5 (8.3) μ broad; all basidia 4-spored. Western North America. *C. polytrichoides*

C. Spores ellipsoid, 7.5-11 μ broad; basidia 2- and 4-spored in about equal proportions. South Africa. *C. liberatum*

B. Spores deep and rich rusty brown under the microscope in ammoniacal medium; cheilocystidia as in *C. Besseyi* but longer (48-70 × 4.5-7.5 μ); basidia all 4-spored. From Wyoming to the Pacific coast *C. cucullatum*

105. CONOCYBE Fayod,

Prodrome, Ann. Sc. Nat., VII. **9**: 357. 1889.

Type species: Galera tenera (Schaeff. ex Fr.) Quél.

Syn.: Galerula Karst., *Bidr. Finl. Nat. Folk* **32**: xxiii. 1879, p. p. [1]

Characters: Habit of the carpophores mycenoid, rarely assuming tricholomatoid appearance and then, because of the color of the lamellae, strongly reminiscent of *Cortinarius*; pileus hygrophanous, glistening when dry, not noticeably gelatinized in its outer layer with piriform to subglobose cells forming the epicutis; dermatocystidia on the stipe often present, but none on the pileus; lamellae usually at first strongly ascendant, the pileus not radially plicate-sulcate along the back of the lamellae but often transparently striate to somewhat sulcate; veil none, or slight on the margin of the pileus, none on the stipe; spore print a deep, rich, beautiful rust color; spores smooth or faintly verruculose, verrucose in some tropical species, with germ pore, deep rust color (rarely paler rusty melleous) in ammonia, lemon-shaped, lentiform, or mostly ellipsoid, in the lentiform spores a hexagonal outline (benzene formula) in frontal view often very marked; basidia broad and short, otherwise variable especially in the number of sterigmata, 2-spored races frequent; cystidia on the sides of the lamellae probably not present in any species but cheilocystidia always present, very characteristic, ventricose below, with a globose capitulum which is stalked abruptly (Pl. XXI, 2); pseudoparaphyses often very striking; hymenium sometimes containing a

[1] The lectotype cannot be referred to either *Galerina* or *Conocybe* because of insufficient data and absence of type specimens.

substance that crystallizes in ammoniacal medium forming long colorless needles; hymenophoral trama reduced to a very thin mediostratum consisting of a few filamentous hyphae which are flanked by the enormously developed hymenopodium consisting of voluminous elements, the hymenopodia of both sides of the mediostratum almost touching each other, the whole trama making almost the impression of being bilateral but the flanking layer not divergent, rather all hyphae more or less parallel with each other; stipe usually straight and central, elongate and thin, rarely thick fleshy, often villous or pubescent, pruinose, etc., from hairs or dermatocystidia (which are often shaped like those of the edge of the lamellae), white or colored, with or without a pseudorrhiza, rarely somewhat marasmioid; all hyphae with clamp connections in the normal (heterothallic) forms. In and outside the woods, not rare in greenhouses, fields and gardens, on the bare soil, or among mosses and grasses, or on decayed wood, on charcoal, on anthills, on dung, etc.

Development of the carpophores : Unknown.

Area : Cosmopolitan.

Limits : The genus *Conocybe* is very sharply separated from all genera of this family if, as proposed by the author since 1948, the genus *Galerella* is recognized as a separate unit between *Conocybe* and *Pholiotella*. In this case, all three genera become very homogeneous and natural and also easy enough to define. *Pholiotina* has a trama quite different from that of *Conocybe;* besides, it has dermatocystidia on the pileus, and more often a veil. The cheilocystidia are capitate only in one single species, and even there not as abruptly as in the Conocybes. This correlation of important characters makes it possible to distinguish a third genus, *Galerella*, where the shape of the cheilocystidia is similar to that in *Pholiotina* while the trama is like that of *Conocybe :* this peculiar combination of characters is supplemented by one more character not observed in either *Pholiotina* or *Conocybe*, the plicate sulcate margin.

State of knowledge : An excellent monograph by R. Kühner has in part been devoted to this genus, and consequently the latter is much better known than *Bolbitius* which has not been monographed. Kühner's monograph includes *Galerina*. The author accepts Kühner's classification of the species of *Conocybe* but raises his subsections of the section *Capitatae* (which coincides with the author's conception of the subgenus *Eu-Conocybe*) to sections, excepting *Farinosae* which become a synonym of the section *Capitatae* sensu stricto. One more

section, and one subgenus are added, both based on species unknown to Kühner. This brings the number of species admitted here to 23. Velenovsky (1947) estimates the number of species of *Galera* (i. e. *Conocybe* and *Galerina*) as 4000 in Europe alone whereas the author admits not more than 43 in the world flora, — quite a contrast !

Practical importance : Unknown.

SPECIES

Subgenus I. **Euconocybe** Sing. (1947). Spores smooth or very indistinctly verruculose, larger than 6 µ; stipe fragile and rather soft, not appearing marasmoid in dried specimens; on the soil in and outside the woods, also on charcoal, dung, sand, foliage, anthills, etc., rarely on decayed wood.

Type species as in genus.

Sect. 1. CAPITATAE Kühner (1935) em. (in the sense of *Capitatae* subsection *Farinosae* Kühner). Stipe entirely covered with cheilocystidia like dermatocystidia (i. e. all capitatae); no hair-like bodies present on the surface of the stipe.

Type species as in the genus and subgenus.

C. laricina Kühner; *C. mesospora* Kühner with several forms and varieties; *C. Rickeniana* Sing. [Galera spicula (Fr.) Quél. sensu Ricken non al.: Conocybe, « (Ricken) » Kühner, non al.] with several forms and one variety; *C. tenera* (Schaeff. ex Fr.) Fayod ex aut. sensu Kühner with several forms and varieties; *C. striatipes* (Speg.) Sing. (C. leucopoda Kühner); *C. antipoda* (Lasch) Kühner (Galerula floridana Murr.)

Sect. 2. MIXTAE Kühner; (1945, ut subsectio). Stipe with cheilocystidia-like (i. e. capitate) dermatocystidia and at same time with hair-lide elements.

C. megalospora J. Schaffer (Galera, J. Schaffer).

Sect. 3. PILOSELLAE Kühner (1935, ut subsectio). Stipe not entirely white, with numerous hair like elements but cheilocystidia-like dermatocystidia (at least such with abruptly capitate apex) none present.

Type species : C. pilosella (Pers. ex Fr.) Kühner.

C. pilosella (Pers. ex Fr.) Kühner (sensu Atkinson, Kühner); *C. anthracophila* (R. Maire & Kühner) Sing. (C. siliginea var. anthracophila Maire & Kühner); *C. neoantipus* (Atk.) Sing. (Galerula, Atk.; C. siliginea var. neoantipus Kühner); *C. plumbeitincta* (Atk.), Sing.

(C. siliginea var. ocracea Kühner [119]); *C. bulbifera* (Kauffm.) Romagnesi; *C. ambigua* (Kühner) Sing. (C. siliginea var. ambigua Kühner); *C. fragilis* (Peck) Kühner sensu Kühner (an Peck); Galera incarnata J. Schaffer); *C. siliginea* (Fr.) Kühner sensu Bres., non Kühner (Galera Quel., Bres.; Galera tenera ssp. siliginea Konr. & Maubl. an sensu Bres.; Galera Rickenii J. Schaffer); *C. magnipora* (Murr.) Sing. (Galerula, Murr.).

Sect. 4. **CANDIDAE** Kühner (1935 ut subsectio). Characters of the surface of the stipe similar to those of section 3, the whole stipe white; pileus often not striate.

Type species: C. lateritia (Fr.) Kühner sensu Kühner.

C. lactea (Lange) Metrod (Galera, Lange; C. lateritia (Batt. ex Fr.) Kühner sensu Kühner: Agaricus, Batt. ex Fr. non Schaeff. ex Fr.; Galera, Quel.); *C. crispa* (Longyear) Sing. (Galera, Longyear), *C. subcrispa* (Murr.) Sing.; *C. crispella* (Murr.) Sing.

Sect. 5. **GIGANTEAE** Sing. (1948). Characters of the surface of the stipe as in section 3 and 4 but the entire stipe white as in section 4 and pileus and stipe very stout for a *Conocybe*, assuming the habit of a *Cortinarius*.

C. intrusa (Peck) Sing. (Cortinarius, Peck).

Subgenus II. **Ochromarasmius** Sing. (1947). Spores sometimes minute, smaller than 6 µ, distinctly warty; stipe sometimes very thin and cartilaginous, looking like that of *Marasmius aciculiformis* Berk. & Curt., covered with capitate dermatocystidia; on decayed trunks and stumps in Brazil.

C. paraensis (Henn.) Sing. (Naucoria, Henn.); *C. macrorhiza* (Speg.) Sing. (Galera, Speg.).

KEY TO THE SPECIES

The best key available is that by Kühner, in *Le Genre Galera* (Fr.) Quél. Paris 1935.

[119] The author differs from Kühner in his interpretation of the species *A. siligineus* Fr. This species is considered identical with what Bresadola called *Galera siliginea*, and what J. Schäffer called *Galera Rickenii* J. Schäffer; consequently what Kühner considers as varieties of his interpretation of *A. siligineus* Fr. and what the author believes are independent species, none of them comparable to Fries' species, had to be raised to specific rank.

106. GALERELLA Earle

Bull. N. Y. Bot. Gard. **5**: 422 1909.

Type species: Agaricus coprinoides Peck.

Characters: Differing from *Conocybe* in the non capitate cheilocystidia and the plicate-sulcate pileus (after the manner of some thin *Coprini*); from *Bolbitius* in non-viscid pileus and smaller spores. On meadows and in the woods.

Development of the carpophores: Unknown.

Area: Temperate and subtropical regions of at least the northern hemisphere.

Limits: See under *Conocybe.*

State of knowledge: Only one species is completely known, others are merely suspected to belong here.

Practical importance: Unknown.

SPECIES

G. plicatella (Peck) Sing. (Agaricus, Peck; Galera, Earle; Galerula, Murr.; Conocybe, Kühner; Agaricus coprinoides Peck; Galera, Sacc.); according to Kühner probably also *Galera crocospora* (Berk. & Curt.) Sacc.; *Galera pulchra* Clements, *Galera flava* Peck, and *Bolbitius coniocephalus* (Bull.) sensu Ricken. These latter species have not been transferred to *Galerella* because they are incompletely known.

107. PHOLIOTINA Fayod

Prodrome, Ann. Sc. Nat., Bot. VII. **9**: 359. 1889

Type species: Pholiota blattaria (Fr.) Gillet.

Characters: Characters same as in *Conocybe* but trama of the lamellae normally regular, i. e. mediostratum more developed and hymenopodium less developed than in that genus; spores always smooth; cheilocystidia rarely ampullaceous-capitate and then not so abruptly as in *Conocybe*; dermatocystidia on the pileus often present; veil often present. On foliage, on decayed wood, on the soil, in and outside the woods.

Development of the carpophores: Probably always hemiangiocarpous.

Area: Cosmopolitan.

Limits: See under *Conocybe.*

State of knowledge : The 14 species now listed in *Pholiotina* are well known. This is mainly due to Kühner's monograph *Le Genre Galera*, Paris 1935.

Practical importance : None.

SPECIES

Sect. 1. **PILIFERAE** Kühner (1935, ut sect. gen. *Conocybae*) Veil none.

Type species : *P. pygmaeoaffinis* (Fr. sensu Kühner) Sing.

P. coprophila (Kühner) Sing. (Conocybe, Kühner); *P. aberrans* (Kühner) Sing. (Conocybe, Kühner); *P. cyanopoda* (Atkinson) Sing. (Galerula, Atk.); *P. Mairei* (Kühner) Sing. (Conocybe, Kühner); *P. pygmaeoaffinis* (Fr. sensu Lange) Sing. (Galera, Lange; Conocybe, Kühner).

Sect. 2. **TOGULARES** Konrad & Maubl. (1924-1937, ut sect. gen. *Pholiotae*). Veil present, appendiculate or annulate.

Type species : *P. togularis* (Bull. ex Fr.) Fayod ex Sing. (sensu Ricken, Kühner).

P. subnuda (Kühner) Sing. (Conocybe, Kühner); *P. septentrionalis* (A. H. Smith) Sing. (Pholiota, A. H. Smith; Pholiota intermedia A. H. Smith non Sing.; Conocybe, Kühner); *P. appendiculata* (Lange & Kühner) Sing. (Conocybe, Lange & Kühner); *P. blattaria* (Fr.) Fayod ex Sing. (sensu Ricken, Kühner), with several formae; *P. vestita* (Fr. apud Quél.) Sing. (Galera, Fr. apud Quél.; Conocybe, Kühner); *P. peronata* (Kühner & R. Maire) Sing. (Conocybe, Kühn. & Mre.); *P. filaris* (Fr.) Sing. (Agaricus togularis var. filaris Fr.; Conocybe, Kühner); *P. rugosa* (Peck) Sing. (Pholiota, Peck); *P. togularis* (Bull. ex Fr.) Fayod ex Sing. (sensu Ricken, Kühner).

KEY TO THE SPECIES

A key is unnecessary since the monograph by Kühner cited above contains a good key to the species of *Pholiotina* (under *Conocybe*), and only one of the species enumerated above (*P. rugosa*) is not keyed out there.

108. TUBARIOPSIS Heim

Le Genre Inocybe, p. 61. 1931.

Type species : *T. torquipes* Heim.

Characters : « Pileus thin, hygrophanous, with straight margin,

with cellular epicutis, formed by subisodiametric elements; stipe inseparable from the pileus, fibrous, fistulose and contorted, elastic; lamellae distant, thick, venose and anastomosing, subdecurrent; spores large, smooth, obovoid, with a broad germ pore, with triple wall, brown; cystidia rare, projecting, not muricate, thin-walled. On the earth ». Heim. The type species has a true epithelium, judging from the figure; the septa are drawn without clamps; the cystidia are shown with ampullaceous apex.

Development of the carpophores: Unknown.

Area: Madagascar.

Limits: According to the data indicated by Heim and quoted above, this genus differs from *Pholiotina* in the large number of globose elements without dermatocystidia in the cuticle, and in the imperfect development of the hymenophore. If *Tubariopsis* is closer to *Cyttarophyllum*, it is certainly well characterized by its epithelium.

State of knowledge: The author has not seen the material on which Heim based his description. However, since obviously all the important characters are indicated, and the fungus does not fit into any of the genera existing until 1931, it may be allowed to insert this genus on the evidence of Heim's description. Only one species is known.

Practical importance: None.

SPECIES

T. torquipes Heim.

109. BOLBITIUS Fr.

Epicrisis, p. 253. 1838

Type species: *B. fragilis* (L. ex Fr.) Fr.

Syn. : *Pluteolus* (Fr.) Gillet, *Hymen. Fr.*, p. 549. 1876
Agaricus subgen. *Pluteolus* Fr., *Hym. Eur.*, p. 266. 1874
Mycena (Pers.) Roussel ex Murr., *North Am. Fl.* **10**: 190. 1917, non (ex Fr.) S. F. Gray.

Characters: Differing from the other genera of this family in plicate sulcate or sulcate margin and opinous to viscid surface of the pileus, noncapitate cheilocystidia, and frequently white stipe.

On dung, sawdust, earth, also on rotten trunks, on straw, on swampy soil, etc.

Development of the carpophores : Probably hemiangiocarpous.

Area : Probably almost cosmopolitan.

Limits : Kühner (1935) sums up the differences between this genus and *Conocybe*, *Galerella*, and *Pholiotina* in the following manner : « It differs from [these genera] at first in the viscid covering of the pileus. The *Bolbitii* which have a pileus that is almost always striate or even split above the dorsal part of the lamellae like that of the veliform *Coprini*, appear to be generally lacking the brownish ocher membrana pigment which is present especially in the lower portions of the stipe in nearly all species of *Conocybe* [*Galerella*, and *Pholiotina*] ; their stipe is white to the base unless it shows — as is very often the case in the pileus — such bright colors as yellow, greenish bluish, violet, or rose ; these colors are intracellular, at least in *Bolbitius titubans* and *B. aleuriatus* whereas the *Conocybe* [Galerellas and Pholiotinas] generally appear to lack all vacuolar pigment. The *Bolbitii* are separated from *Conocybe* anatomically by their [homogeneously] regular [hymenophoral] trama and by the pseudoparaphyses which are often more developed » (Pl. XIII, 1).

Since there are species in *Bolbitius* which have dull brown (not really rusty) spore print, for instance one species recently collected by the author in Virginia with « Cochin » (Maerz & Paul) spore print on white paper (perhaps *B. nobilis* Peck), there is also need of separating *Agrocybe* from *Bolbitius* on the basis of other characters than the color of the spore print. However, the distinguishing characters indicated in the generic key (p. 479) will be sufficient in all cases to avoid confusion between the two genera.

State of knowledge : The genus *Bolbitius* is very little known. It has not been monographed, and the distinguishing features of the European species are very weak. In other parts of the world where there are many more species of *Bolbitius*, the situation is even worse. In the eastern states of the U. S. A., several species can be found which appear to be omitted in the floras, and will probably turn out to be new. A monograph of the American species is most urgently needed. Only five species are admitted below, but many more species exist.

Practical importance : None.

SPECIES

Stirps **Reticulatus** (On wood; usually without yellow pigment and and not entirely white).

B. reticulatus (Pers. ex Fr.) Ricken; *B. aleuriatus* (Fr.) Sing. (Pluteolus, Karst.).

Stirps **Vitellinus** (On pastures, on dung or sawdust, etc., often white or yellow).

B. vitellinus (Pers. ex Fr.) Fr. [Bolbitius fragilis (L. ex) Fr.; Bolbitius titubans (Bull. ex Fr.) Fr.]; *B. exiguus* Sing.; *B. albiceps* Speg.

According to Kühner, the following species also belongs in *Bolbitius*: *B. glaucopurpureus* (Berk. & Br.) Kühner [Agaricus (Galera), B. & Br.].

According to Murrill, the number of species in *Pluteolus* and *Bolbitius* as cited in *North America Flora* 10: 186-193. 1917, is twenty seven. Some of those most likely to be true *Bolbitii* are: *Pluteolus glutinosus* Clements; *Mycena variicolor* (Atk.) Murr. (recte: *Bolbitius variicolor* Atk.); *Pluteolus coprophilus* Peck, etc. but only the latter has been restudied in a modern way, otherwise one has to depend on the descriptions available until new type studies uncover the facts now missing.

KEY TO THE SPECIES

Under the circumstances, a new key to the species of *Bolbitius* would not be of much value.

150. **AGROCYBE** Fayod

Prodrome, Ann. Sc. Nat. VII. 9: 358. 1889

Type species: *Pholiota praecox* (Pers. ex Fr.) Quél.

Syn.: *Ratea* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 424. 1909
Togaria W. G. Smith, *Brit. Basid.*, p. 122. 1908 emend. Romagnesi, *Rev. Mycol.* 2: 178. 1937
Pseudodeconica Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 19. 1927, nom. nud.

Characters: Pileus comparatively fleshy, not sulcate-plicate but either entirely striate or very finely transparentely striate over a very short distance from the margin toward the center, with a hymeniform covering forming the epicutis and consisting of globose or short piriform cells; lamellae broad (moderately broad to extre-

mely broad), either with cystidia on both the sides and the edge of the lamellae or with cheilocystidia only; basidia 2-3-, or 4-spored, otherwise normal; spore print « Cochin », « burnt umber », « chocolate », « Montella », « Mandalay », or even darker in the same tone (Maerz & Paul): spores under the microscope melleous with a dark chestnut ferruginous hue, smooth, with thick double wall, with germ pore (which is either broad and truncate or narrow and non truncate, and then often easily overlooked and indistinct,, in some species with a majority of pore less spores in a print, in other species spores with 2 3 germ pores occasionally observed; stipe white or colored, smooth or rough, with or without veil, the latter often well developed and leaving an annulus on the mature stipe, base of the stipe often connected with thin white rhizomorphs (rhizoids); context consisting of hyphae with clamp connections. In the woods and more often outside the woods, in gardens, on lawns, on fields and meadows, on the earth and on dung, seeds, rotting *Cormophyta*, also in greenhouses on manured soil, on anthills and on decaying wood.

Development of the carpophores: Unknown for most of the species, in some hemiangiocarpous.

Area: Almost cosmopolitan.

Limits: Considering the close relationship between certain veiled and certain naked forms, and also the fact that many veiled species occasionally occur without any veil, the author does not think that the revival of the genus *Togaria* in the sense of Romagnesi is needed. Aside from that, the type species proposed by Romagnesi does not occur in W. G. Smith's first account and, consequently, cannot be accepted.

State of knowledge: This genus is taxonomically rather difficult, at least the innumerable forms around *A. pediades* and *A. semiorbicularis* on one hand, and *A. erebia* on the other. This genus is also in need of monographic treatment. The author has once made an (unpublished) study on the average sizes of the small, normal and gigantic spores occurring in a spore print, and the quotients of hundreds of measurements of length as well as breadth of the spores, were expressed in curves which, in turn were compared in the various species and forms It is possible that this method will in the end be of some assistance in the delimination of forms or species. The results obtained by the author showed very distinct differences in various forms investigated but the question whether or not these differences follow specific lines could be answered only tentatively.

Consequently, the species enumerated below and the key are not based on biometrical data. Seventeen species are admitted.

Practical importance: Several species of *Agrocybe* are excellent edible mushrooms. Some have been cultivated by the peasants in Southern Europe, especially in Italy, by a rather primitive method, mainly by watering naturally infected trunks. The most important of these species is *A. Aegerita,* but *A. dura* and *A. praecox* are also edible.

SPECIES

Subgenus I. **Eu-Agrocybe** Sing. (1936). Spores distinctly truncate, with broad germ pore. Carpophores developing on the ground, and on various kinds of vegetable matter, not on living or freshly cut wood.

Type species: *A. praecox* (Pers. ex Fr.) Fayod ex aut.

Sect. 1. **PEDIADEAE** (Fr.) Sing. (1936) (Gen. *Naucoria,* sect. *Pediades* Lange 1938). Veil usually none, very rarely annular; cystidia none except cheilocystidia.

Type species: As in the subgenus.

A. pediades (Pers. ex Fr.) Fayod ex aut., and several closely allied species or races [such as *A. semiorbicularis* (Bull. ex Fr.) Fayod ex aut., *A. amoena* (Weinm.) Sing., *A. arenicola* (Berk.) Sing. and *A. fimicola* (Speg.) Sing. (*Naucoria,* Speg.) = *N. subamara* Murr. p. p.] *A. arvalis* (Fr. sensu W. G. Smith) Sing.; *A. vervacti* (Fr.) Romagnesi sensu Lange, Romagnesi, non Sydow, nec al.

Sect. 2. **PRAECOCES** (Konr. & Maubl.) Sing. (1936) (*Pholiota* sect. *Praecoces* Konrad & Maubl. 1924-37). Veil present; cystidia present on the sides of lamellae.

Type species. *A. praecox* (Pers. ex Fr.) Fayod ex aut.

A. Puiggarii (Speg.) Sing. (Pholiota, Speg. sensu Rick.); *A. floridana* (Murr.) Sing. (Pholiota, Murr.); *A. Howeana* (Peck) Sing. (Pholiota, Sacc.); *A. dura* (Bolt. ex Fr.) Sing. [Pholiota, Quél.; Pholiota vermiflua (Peck) Sacc.]; *A. praecox* (Pers. ex Fr.) Fayod ex aut.; *A. acericola* (Peck) Sing. (Pholiota, Sacc.); perhaps also *A. gibberosa* (Fr.) Sing. at least sensu Sing.

Sect. 3. **MICROSPORAE** Sing. (1936). Veil none; cystidia present on the sides of the lamellae, or spores not larger than 13 µ, usually smaller than 10 µ.

Type species: *A. tuberosa* (Henn.) Sing.

(Fr.) Quél. sensu Heim & Romagnesi, non Fr.; Agrocybe, Sing.; Agaricus arvalis Fr. sensu Libert non Fr.; Galera arvalis var. tuberigena Quél.; Naucoria sclerotina Vel.] with var. *heterospora* Sing.; *A. putaminum* (R. Maire) Sing. (Naucoria, Maire); *A. amara* (Murr.) Sing. (Naucoria, Murr.); *A. retigera* (Speg.) Sing. (Naucoria, Speg.; Naucoria semiorbicularis var. lacunosa Murr.); *A. collybiiformis* (Murr.) Sing. (Naucoria, Murr.).

Subgenus II. **Aporus** Sing. (1936) (*Ombrophila* Sing. 1936). Germ pore often indistinct, or spores not always distinctly truncate.

Type species: *A. Aegerita* (Brig.) Sing.

Sect. 4. VELATAE Sing. (1938). Veil present, usually distinctly anuliform.

Type species: *A. erebia* (Fr.) Kühner.

A. erebia (Fr.) Kühner (Pholiota, Quél.) and allied species (such as *Pholiota aggericola* (Peck.) Sacc., *P. washingtoniensis* Murr., *P. ombrophila* (Fr.) Karst. etc.]; *A. Aegerita* (Brig.) Sing. [Pholiota, Quél.; Pholiota cylindracea (D. C. ex Fr.) Gillet; Pholiota crassivela (Speg.) Sacc.; Pholiota impudica Speg.]

Sect. 5. EVELATAE Sing. (1948). Veil none.

A. firma (Peck.) Sing. (Naucoria, Peck.).

KEY TO THE SPECIES

A. Germ pore of the spores distinct, broad; apex of the spores always distinctly truncate.

B. Cystidia vesiculose or broadly ampullaceous, or with finger like appendages, occurring on the sides of the lamellae as well as on the edges.

C. Veil distinct, usually anuliform, very rarely missing in certain individual carpophores.

D. Many spores up to 14.5 μ long; pileus white or rather strongly colored in most specimens. Temperate regions, and also in the subtropics.

E. Pileus strongly colored.

F. Pileus not becoming testaceous; taste bitter. North America — *A. Howeana*

F. Pileus becoming testaceous; taste (?) mild. South America. — *A. Puiggarii*

E. Pileus white or very pale colored — *A. dura*

D. Spores considerably smaller than 14.5 μ, few of them larger than 10 μ.

G. Most spores rhomboid-subangular in frontal view; most frequently on or near stumps and trunks or at least growing on forest humus. North America — *A. acericola*

G. Most spores not much different in shape whether they are

seen in frontal or in lateral view (in profile). Widely distributed species of the open places, or else woodland-species of Florida.

H. Cystidia evenly rounded above but pedicellate; on humus and on decayed logs in hammocks in Florida. *A. floridana*

H. Cystidia different; preferring open and semi-open places, widely distributed. *A praecox*

C. Veil always absent.

I. Cystidia with finger-like appendages, or at least many of them appendiculate; stipe mostly rising from a sclerotium. *A. tuberosa*

I. Cystidia without appendages; sclerotia none.

J. Spores 8 13 × 5-7 μ; pileus smooth.

K. Pileus distinctly colored; context somewhat bitter; not growing on sawdust.

L. Cystidia with calcium oxalate crystals incrusting the apices; context of the stipe fulvous; lamellae rather narrow for an *Agrocybe:* taste somewhat bitterish On seeds of *Prunus Cerasus* in France. *A. putaminum*

L. Cystidia not or little incrusted at the apex; context of the stipe whitish; taste decidedly bitter and somewhat astringent. Not on seeds New York. *A. amara*

K. Pileus little pigmented, milkwhite, etc; context mild. On sawdust in Florida. *A. collybiiformis*

J. Spores (11) 13-14 (16.5) × (7) 7.5 (8.7) μ; pileus scrobiculate in the marginal portion. On sandy soil in Florida and Paraguay. *A. retigera*

B. Cystidia none on the sides of the lamellae; cheilocystidia narrowly to moderately broadly ampullaceous with a slight subcapitate thickening at the tip of the « neck » in most cases; veil usually none or inconspicuous.

M. Spores larger than 10 μ, up to 18 μ long.

N. Ovoid bulb of the base of the stipe continuing into long and solid rhizomorphic strands (white); pileus fulvous yellow, becoming brownish; spores 1.45 to 1.70 times longer than broad, comparatively broader in younger and smaller spores than in older and larger spores; lamellae moderately broad; stipe brownish to beautifully ochraceous brown. Usually in fields. Europe *A. arvalis*

N Stipe radicate or not; pileus often paler; spores broader than indicated above, or as broad but then becoming comparatively broader in age (i. e. when fully mature and the largest spores of the print); stipe less colored, most frequently almost white. In fields and meadows, also in steppes and prairies, on grassy mountain sides, usually on soil, sand, or dung.

M. Spores smaller than 10 μ. *A. vervacti*

N. Germ pore indistinct because of the non-truncate apex of the spores, or else narrow and not always clearly visible in all spores of a print

O. Veil present, annuliform in most cases.

P. Pileus rather dark brown in young and fresh specimens, sometimes almost black in the center; spores often elongate and norrow, rather large, and then basidia 2-spored. On the ground, among foliage and on very decayed frondose wood. *A. erebia* and allied forms

P. Pileus chamois or more fulvous ochraceous, not very deeply colored even when young; spores not as described above; growing on the base and in wounds of living trees and on freshly felled trunks. *A. Aegerita*

O. Veil none. North America *A. firma*

STROPHARIACEAE Van Overeem ex Sing. & Smith

Mycologia **38**: 503, 1946; Van Overeem, *Bull. Jard. Bot. Buitenzorg* **9**: 19, 1927, nom. nud.; Romagnesi, *Rev. Mycol.* **2**; 243, 1937, nom. nud.

Type genus: Stropharia (Fr.) Quél.

Characters: Epicutis of the pileus always consisting of thin hyaline filamentous, clamped strictly repent hyphae; hypodermium often subcellular; hymenophore lamellate; lamellae adnexed, sinuate, adnate, or adnate-decurrent; spore print deep lilac to blackish lilac, or else cinnamon brown, deep rusty cinnamon, or deep fuscous sepia with, perhaps, a slight purplish hue; spores under the microscope melleous to chestnut, often with a deep reddish chestnut line around the episporium, the wall always well differentiated into endo- and a smooth episporium and rarely continuous at the apex, usually with a more or less broad germ pore and sometimes, especially in the genera with lilac spore print, distinctly truncate; cystidia present only on the edges (cheilocystidia), or else also scattered to numerous on the sides of the lamellae, in the latter case, they belong most frequently to a special type of cystidia, called chrysocystidia (Pl. XVII, 3), with an amorphous body in the broadest portion of the cystidium, this body turning more or less strongly yellow in NH_4OH, the shape of the chrysocystidia always characteristic, clavate or clavate-mucronate; context always soft fleshy and not light in weight and dry, never tough, but often bitter to the taste; all hyphae with clamp connections. On a great variety of substrata, in deep moss, on living or decayed wood, on charcoal, on the rhizomes of living *Pteridophyta*, on foliage and needles, on palm detritus, dead *Gramineae* and other herbaceous stems, fruits, etc., on living grass

roots, exposed tree roots, on dung, and on the earth; in open fields, pastures, gardens, etc., and also in the woods, hammocks, tundras, and swamps.

Limits: The limits of this family are obvious. The species with very narrowly adnexed lamellae and scaly pileus which would have been considered as belonging in *Stropharia* but have some characters of *Agaricus* are in need of further study. The dry, tough gastromycetoid forms are taken to the *Bolbitiaceae* which are otherwise clearly separated from the *Strophariaceae* by having a cellular epicutis. The *Cortinariaceae* with smooth spores are distinguished from the *Strophariaceae* by the complete lack of a germ pore in the spores and or the structure of the cuticle. The pleurotoid genera, viz. *Pleuroflammula* and *Melanotus* have formerly been confused with *Crepidotus* (*Crepidotaceae*) but differ in germ pore, brighter or more deeply fuscous spore print, more conspicuous and longer cheilocystidia than in the smooth-spored *Crepidoti*, and the presence of a fugacious veil in many of these strophariaceous forms; they also have constantly numerous clamp connections, repent epicuticular hyphae and homogeneous trama of the pileus whereas many *Crepidoti* with smooth spores have clampless septa and gelatinous layers.

Stropharia, the type genus of the *Strophariaceae* has formerly been combined (Fries) with *Agaricus*, the type genus of the *Agaricaceae*. The two families can, however, be distinguished, on this level, by the attachment of the the lamellae, the shape of the cheilocystidia, the presence or absence of clamp connections, the size of the basidia and some chemical characters.

The *Coprinaceae* differ in having autodeliquescent lamellae of the inaequihymeniiferous type, or else a distinctly cellular epicutis. The color of the spore print is also different in the two families.

Pleurotoid forms do not occur in the preceding families with colored spores. However, they do occur in the following families, from the *Cortinariaceae* to the *Paxillaceae*. But all the other pleurotoid chromosporous agarics lack the germ pore.

The *Strophariaceae* come closest to the *Cortinariaceae* on the level of certain small species of *Pholiota* which may remind one of *Phaeomarasmius* (but the differences are still very striking, see under « Limits » in the latter genus) and one species of *Pleuroflammula*, *P. flammea* which comes close to a group of species called *Flavidula* by Romagnesi (nom. nud.), and the small genus *Pyrrhoglossum* where the spores are warty.

KEY TO THE GENERA

A. Chrysocystidia present.

B. Hypodermium consisting of elongate hyphae which are broader than the hyphae of the epicutis but do not form a subcellular layer; veil always annular, simple or double, dry or glutinous; spores usually small (up to 10 μ long), in two species longer (reaching more than 20 μ in length); cheilocystidia most frequently clavate; growing on the soil or on dung, rarely on other habitats. 111. *Stropharia*

B. Hypodermium subcellular, consisting of intermixed hyphae and subisodiametric cells or spherocysts with the latter often predominant; annulus simple, or none and then the veil restricted to the margin (as far as mature specimens are concerned), rarely very fugacious and not showing up in mature specimens; spores either small or large; growing on the soil or on moss or on wood, etc. 112. *Naematoloma*

A. Chrysocystidia none.

C. Spores very large; pileus and stipe viscid, the latter viscid from a glutinous subannulate veil; occurring on manured soil or on dung (see *Stropharia*)

C. Spores small to very large; pileus sometimes somewhat viscid but veil never glutinous, occurring on dung or on other habitats.

D. Spores larger than 10 μ; pleurocystidia present, or veil annulate or spores definitely not lentiform (or more than one of these three characters combined), stipe always central and more or less straight or somewhat flexuous, usually rather long, sometimes with a pseudorhiza; pileus hygrophanous or non-hygrophanous. 113. *Psilocybe*

D. Spores up to 10 μ long, stipe rarely with an incomplete annulus, usually exannulate; pleurocystidia always absent, spores sometimes strongly lentiform; stipe sometimes short, curved, and eccentric, pseudorrhiza none; pileus hygrophanous

E. Stipe centrally attached and as long or longer than the diameter of the pileus, spores very broad in frontal view and heart shaped to rhombic, but when turned around the longitudinal axis so as to be seen in profile, they are much (0,7-1,3 μ) narrower and ellipsoid. 114. *Deconica*

E. Stipe little developed, short (much shorter than the diameter of the pileus) curved and often not free from the rear side of the pileus, eccentric; spores very slightly to not lentiform 115. *Melanotus*

111. STROPHARIA (Fr.) Quél.

Champ. Jura Vosg., p. 141, 1872-3

Type species: *S. aeruginosa* (Curt. ex Fr.) Quél.

Syn.: *Agaricus* trib. *Stropharia* Fr., *Summ. Veg. Scan.*, p. 295, 1849.
Geophila Quél., *Enchiridion*, p. 111, 1886.

Psalliota subgenus *Stropharia* (Fr.) Schröter in Cohn, *Krypt. Fl. Schles. Pilze* 1 : 537. 1889.
Stercophila Romagnesi, *Rev. Mycol.* 1 : 36. 1936, nom. nud.

Characters : Pileus humid or viscid; epicutis consisting of repent filamentous hyphae; hypodermium not subcellular; lamellae adnexed to adnate, usually broad; trama regular but becoming irregular in age; chrysocystidia present (Pl. XVII, 3), rarely absent, and then the stipe covered by a glutinous veil; cheilocystidia always present and well differentiated making the edge of the lamellae heteromorphous; spore print deep lilac to blackish lilac (when fresh), becoming duller colored by slow dehydration in the herbarium, usually lilac when young and examined in water under the microscope but later (and in other media) tending to be fuscous or olive, often with a chestnut colored line along the episporium, smooth, very strongly double walled, the wall thick and consisting at least of an episporium and an endosporium, always with a distinct germ pore, strongly truncate at the apex, more rarely non truncate, usually small, but in two species very large; stipe central, straight or somewhat flexuous, longer than the diameter of the pileus, always annulate, the veil usually membranous but in two species entirely glutinous, consisting of a gelatinous mass in which some filamentous hyphae are imbedded; on the soil and on dung, rarely on other habitats.

Development of the carpophores : Hemiangiocarpous.

Area : Almost cosmopolitan.

Limits : This genus is somewhat smaller than it was in the original sense as used by Saccardo. However, if the veil is made the leading differentiating character, the group resulting will be neither natural nor sharply separable. The presence of chrysocystidia is also not an ideal character but it coincides much more with the natural limits of the group of which *S. aeruginosa* is the type. In fact, if one exception to the rule (that Stropharias must have chrysocystidias) is admitted, the genus can be satisfactorily separated from *Psilocybe*, *Deconica* and *Melanotus*.

The limits between *Stropharia* and *Naematoloma* are also not difficult to establish if anatomical characters are admitted as the basis of delimitation. The species of the genus *Naematoloma* as understood here, are all characterized by a regular hymenophoral trama, even in old carpophores; the hypodermium is subcellular, and the habitat is often different from that of the Stropharias. There are no real transitions between the two genera as outlined in the key, unless

Naematoloma subericaeum and *N. subumbonatescens* with less strongly developed subcellular hypodermium are considered as such.

The delimitation of *Stropharia* is less difficult within the framework of the *Strophariodeae* than within the *Strophariaceae* as a whole. Some species are ambiguous between *Pholiota* and *Stropharia* since they have the characters of one of the genera but the spore color intermediate between the two. *Pholiota malicola* is one of these species and *Stropharia Johnsoniana* is another. The spore print of the latter is « sepia » to « coffee » (Maerz & Paul), i. e. obviously different from that of the *Pholiotoideae* as well as that of *Stropharia*. *Pholiota malicola* has the spore print of a typical representative of the *Pholiotoideae*, yet when the spores are studied in KOH, they are a deep dusky olivaceous as in the *Strophariodeae*. Another case is *Stropharia Kauffmanii* which is said to have « Army brown » (R.) spore print (A. H. Smith) which is not rusty enough for the *Pholiotoideae* and rather aberrant for *Stropharia*.

In cases like those just cited it would appear to be appropriate to disregard minor differences in the spore color if all the other characters of the particular species point to close relationships, or affinity with other species of a genus. Consequently, the author continues to consider *Stropharia Johnsoniana* as a *Stropharia*, and *Pholiota malicola* as a *Pholiota*. As far as *Stropharia Kauffmanii* is concerned, this is a species quite aberrant in several regards, and perhaps not congeneric with any of the established genera of the *Strophariaceae*. The author has not studied the type or any other specimen of that species, and the descriptions available are not fully sufficient for a final arrangement, yet there are indications that might point at an intermediate position beween *Stropharia* and *Agaricus*. Future investigations will clarify this problem.

It may be assumed that the pigmentation of the spores is subject to comparatively recent mutation. This means that the taxonomist has to watch out for exceptional spore colors in order to avoid transfer of the respective species to a group where it does not belong according to the sum of its other characters.

State of knowledge - The genus is comparatively well known but there is no doubt but that monographic studies, especially in non European countries will prove the existence of many undescribed species. Many valuable contributions to the knowledge of this genus were made indirectly (discussing the limits between *Naematoloma* and *Stropharia*) by R. Kühner, and many more species were describ-

ed as new, or redescribed by A. H. Smith in North America. The author limits the list of species admitted to the sections indicated below, to nine.

Practical importance: Though some of the species are considered as edible, they are not eaten much.

SPECIES

Sect. 1. **MUNDAE** (Fr. emend. Fayod 1889) Konr. & Maubl. 1924-37. Pileus subviscid or merely humid, never truly viscid to glutinous; carpophores usually growing in open fields and on meadows rather than in the woods.

Type species: S. coronilla (Bull. ex Fr.) Quel.

S. melasperma (Bull. ex) Quél.; *S. coronilla* (Bull. ex Fr.) Quél.; *S. Johnsoniana* (Peck) Peck (Pholiota, Atk.).

Sect. 2. **PHOLIOTIDEAE** (Fr. 1836 ut sect. *Agarici* subg. *Psalliotae*) Sing. em. (*Viscipelles* Fr. 1854; *Aeruginosae* Fayod 1889). Pileus truly viscid to glutinous; carpophores often growing in the woods, hedgerows, under deep herbaceous growth and under ferns near forested areas, etc.

Type species: S. aeruginosa (Curt. ex Fr.) Quél.

S. aeruginosa (Curt. ex Fr.) Quél.; *S. inuncta* (Fr.) Quél.; *S. albonitens* (Fr.) Karst.

Sect. 3. **STERCOPHILA** (Romagnesi 1936) Sing. Pileus truly viscid to glutinous; stipe also glutinous from an entirely glutinous veil, subannulate; chrysocystidia not always present; spores enormously large; on dung and on manured fields and meadows.

Type species: S. semiglobata (Batsch ex Fr.) Quél.

S. semiglobata (Batsch ex Fr.) Quél.; *S. stercoraria* (Bull. ex Fr.) Quel.; *S. luteonitens* (Vahl. in Fl. D. ex Fr.) Quel.

KEY TO THE SPECIES

The limited number of species indicated here can also be determined by direct consultation of the original and emended descriptions, or by using the keys and illustrations of such general works as Lange's *Flora Agaricina Danica*, or Kauffman's *Agaricaceae of Michigan*.

112. NAEMATOLOMA Karst.

Hattsr., Bidr. Finl. Nat. Folk **32** : xxv. 1879

Type species : N. sublateritium (Fr.) Karst.

Characters : Pileus non hygrophanous or slightly hygrophanous in the marginal portion, usually with rather bright (yellow, fulvous, olive-yellow, purple) colors, not viscid, rarely viscid, usually with a thin appendiculate veil; epicutis consisting of hyaline, filamentous, repent, slightly gelatinized hyphae with clamp connections, partly disappearing in adult specimens; hypodermium subcellular in most species, rarely little developed and consisting of a thin layer of elongate hyphae; with a few shorter hyphae intermixed; lamellae more or less adnexed, adnate or with decurrent tooth, neither deeply decurrent nor free; cystidia present, many of them, mostly all, on the sides of the lamellae, belonging to the type known as chrysocystidia, clavate or clavate mucronate, with a yellow (in NH_4OH) amorphous, refringent body in the widest portion; hymenophoral trama strictly regular and remaining rather decidedly regular even in old specimens; spore print as in *Stropharia*, rarely (in *N. elongatipes*) « cocoa »; stipe centrally attached, often rather long in adult specimens, usually exannulate, rarely with a narrow to well developed annulus (in one small section of the genus), somewhat fibrous and slightly tough to normally fleshy fibrous, usually becoming hollow in age, often becoming brownish or deep fulvous from the base upward, sometimes with a pseudorrhiza, sometimes densely cespitose-fasciculate; context often bitter, hyphae often divided by an amorphous mass of yellow intercellular pigment, all hyphae with clamp connections. On dead and living wood, also on *Sphagnum, Polytrichum, Carex,* on the forest soil among needles, on charcoal, on imbedded sticks and logs, etc.

Development of the carpophores : Hemiangiocarpous.

Area : Almost cosmopolitan.

Limits : Stropharia differs from *Naematoloma* by the non cellular hypodermium and their regular hymenophoral trama in adult specimens; *Psilocybe* differs in the absence of the subcellular hypodermium and the absence of chrysocystidia.

The distinction between *Naematoloma* and *Pholiota* is at times difficult because of the existence of a group of species with spore colors as in *Pholiota* but with a habit characteristic for *Naematoloma,*

sect. *Psilocyboides*. About the separation of this latter group from *Pholiota* subgenus *Phaeonematoloma*, see p. 517-518.

State of knowledge : The European species are well known and most of them occur also in North America and in large parts of Asia. Kühner (1936) contributed much to our present knowledge of *Naematoloma*, especially section *Psilocyboides*. In the survey of the species below, 14 species are recognized. More type studies wills reveal a larger number of species in the future.

Practical importance : N. fasciculare and other species growing on wood may occasionally act as wood destroyers and even contribute to the death of trees in the forest and in plantations. Some species, such as *N. sublateritium*, are frequently used as food by Italians in Europe and North America. Though none of the species is at present considered poisonous, some are extremely bitter and apt to spoil a meal if confused with some of the edible wood-inhabiting agarics.

SPECIES

Sect. 1. **STROPHOLOMA** Sing. (1948). Spores medium or large (often larger than 10 μ); annulus well developed, thick, membranous. On the forest soil, more rarely on sticks and logs, and rarely in deep moss; carpophores often rather thick, large, and fleshy, especially the stipes (as compared with the diameter of the stipes in sect. 2, and especially sect. 3).

Type species : N. squamosum (Pers. ex Fr.) Sing.

N. squamosum (Pers. ex Fr.) Sing. (Stropharia, Quél.) : *N. Hornemannii* (Fr. ex Fr.) Sing. [Stropharia, Lundell & Nannfeldt ; Stropharia depilata (Pers. ex Fr.) Quél.]; *N. Ferrei* (Bres.) Sing. (Stropharia, Bres. ; Stropharia rugosoannulata Farlow).

Sect. 2. **FLAMMULOIDES** Quél. (ut sect. gen. *Dryophilae* 1886) (= *Hypholoma*, sect. *Cespitosa* K. & M. 1948). Spores small (well below 10 μ); annulus inconstant, and if present, not well developed; carpophores sometimes thick and large, sometimes smaller and thin, usually growing in dense fascicles on wood.

Type species : N. fasciculare (Huds. ex Fr.) Karst.

N. elaeodes (Fr.) Konr. & Maubl. (Hypholoma, Gillet); *N. sublateritium* (Fr.) Karst. [Hypholoma, Quél. ; Agaricus lateritius Schaeff. ex Fr. non Batt. ex Fr. ; Hypholoma perplexum (Peck) Sacc.]; *N. capnoides* (Fr.) Karst. (Hypholoma, Quél.); *N. epixanthum* (Fr.) Karst.

(Hypholoma, Quel.); *N. radicosum* (Lange) Konr & Maubl. (Hypholoma, Lange). *N. fasciculare* (Huds. ex Fr.) Karst. (Hypholoma, Quél.).

Sect. 3. **PSILOCYBOIDES** Sing. (1948) (= *Hypholoma*, sect. *Tenuioria* Konr. & Maubl. 1948) Spores often larger than 10 µ; annulus none, or rarely inconstantly and weakly developed; stipe usually rather thin, flexuous and elongate; carpophores mostly solitary or gregarious, not (or exceptionally) fasciculate; on small logs and sticks, more often in deep moss, especially *Sphagnum* and *Polytrichum*, in marshy prairies and in humid forests, also in the subalpine shrub vegetation, in tundras and peat swamps.

Type species: *N. dispersum* (Fr.) Karst.

N. dispersum (Fr.) Karst. (Hypholoma, Quél.); *N. Polytrichi* (Fr. sensu Ricken) Sing. (Hypholoma, Ricken); *N. elongatipes* (Peck) Sing. [Psilocybe, Sacc.; Hypholoma, A. H. Smith; Agaricus (Psilocybe) udus var. elongatus Fr. (?)]; *N. subumbonatescens* (Murr.) Sing. (Stropharia, Murr.); *N. ericaeum* (Pers. ex Fr. sensu Kühner) Sing. (Psilocybe, Quél.; Hypholoma, Kühner); *N. subericaeum* (Fr.) Sing. (Psilocybe, Sacc.; Hypholoma, Kühner).

KEY TO THE SPECIES

The third section can be determined (as far as European species are concerned) by Kühner's key (*Bull. Soc. Myc. Fr.* **52**: 17-30. 1936). The species of section 2 are comparatively easy to determine by most current keys, and the three species indicated here as belonging to section 1 can be looked up in the literature and distinguished by macroscopical characters.

113. **PSILOCYBE** (Fr.) Quel.

Champ. Jura Vosg. p. 147. 1872-3, em.

Type species: *Agaricus semilanceatus* Fr.

Syn.: *Pholiotella* Speg., *Bol. Acad. Cordoba* 11: 412. 1889.

Characters: Pileus cylindric conic or semiglobate to convex, campanulate, often umbonate or papillate, subviscid, or viscid, or hygrophanous, or dry; epicutis consisting of thin, hyaline, filamentous, repent, somewhat to rather strongly gelatinized, thin-walled, clamped hyphae; hypodermium consisting of hyphae somewhat broader than those of the epicutis but not subisodiametric in any case, pig-

mented, rather strictly radially arranged; subcuticular layer consisting of intermixed-irregular elements as most of the context of the pileus; veil slight, fibrillose on the marginal zone of the pileus, often fugacious, or appendiculate, or else absent; lamellae broad, adnexed to adnate, sometimes with a slight decurrent tooth; cheilocystidia present; pleurocystidia present or absent but never any chrysocystidia present on either edges or sides of the lamellae; hymenophoral trama subregular; spore print deep lilac to fuscous sepia; spores with double wall and germ pore, smooth, small to large; stipe dry, glabrous or with a fibrillose coating, often with a distinct well developed annulus, usually strongly elongate and narrowly hollow but in some species frequently thick and fibrillose fleshy, sometimes with a pseudorrhiza; context sometimes bluing and then strongly reacting with monomethylparamidophenol, in other species flesh unchanging and reaction indistinct; odor raphanaceous or farinaceous (not with the astringent, « bitter » odor of *Naematoloma*); all hyphae with clamp connections; on sticks, stems, mud, peat, earth, forest humus, deep moss beds, on scattered dung, sawdust, etc.

Development of the carpophores : At least in some species hemiangiocarpous.

Area : Almost cosmopolitan.

Limits : This genus has been emended by Singer (1936, and again in the present work) in order to be adapted to the diagnosis of the group into which *P. semilanceata* (Fr.) Quél., the type species of the genus, belongs. Many species of the old conception originated by Fries, are now part of the large genus *Psathyrella*, others have been transferred to *Naematoloma*, and one forms the genus *Panaeolina* (this corresponds to the Fayodian emendation of *Psilocybe*). The species left are now combined with certain atypical species of the genus *Stropharia* sensu lato, characterized by the lack of chrysocystidia. Though Fries originated the artificial group *Psilocybe* which was gradually transformed into a natural unit by drastic transfers of species and whole groups of species, he undoubtedly had a vision of the true affinities when he states, under *Agaricus semilanceatus*, that this species continues the *Merdarii* of *Stropharia* (*S. semiglobata* and its allies, and *S. merdaria*), a group that is now divided between *Stropharia* and *Psilocybe*. Fries often surprises the modern taxonomist by short observations on the true affinity of certain groups while at the same time he refuses to express these affinities

Some species of *Naematoloma* which are deprived of a true subcellular hypodermium, nevertheless are provided with chrysocystidia, and are therefore easily separable from the genus *Psilocybe.*

Some authors, even in recent works, have considered *Deconica* as the same genus as *Psilocybe,* or, if two groups are separated, they have not been considered as worthy of generic status. It appears to the author that these genera are separable on the basis of a character which is very easy to observe, viz. the shape and size of the spores. This one character is always correlated with at least one alternative character, i. e. in *Psilocybe*, the spores are either larger than 11 µ or non lentiform, and at the same time, the pileus is non hygrophanous, or the veil is strongly annuliform, or else pleurocystidia are present. The true Deconicas are very uniform macro- and microscopically; they can easily be recognized in the field as belonging to a particular group, and they are related but undoubtedly separable from *Psilocybe* as well as *Melanotus.*

State of knowledge . This genus is in need of a monographic treatment. Only eight species are admitted below which are completely known; some others, especially American species, are in the process of being worked up by A. H. Smith who has begun to publish on them. There are probably many more species in North America, and also in Asia.

Practical importance : At least one species is used as a drug in Mexico (causing a temporary narcotic state of hilarity) but is poisonous when used in excess.

SPECIES

Sect. 1. **MERDARIAE** (Fr. ut subsect. *Agarici* subg. *Strophariae* 1874) Sing. Pileus neither acute nor conic campanulate; veil present, sometimes annuliform; cystidia on the sides of the lamellae present or absent; spores up to 13 µ long; context not bluing on exposure; monomethylparamidophenol reaction weak or none. On dung or on manured fields.

Type species : P. merdaria (Fr.) Ricken.

P. merdaria (Fr.) Ricken (Stropharia, Quél.); *P. coprophila* (Bull. ex Fr.) Quél. (Deconica, Karst.) : *P. blattariopsis* (Speg.) Sing. (Pholiotella, Speg.).

Sect. 2. **CAERULESCENTES** Sing. (1948). Pileus neither acute nor conico campanulate; veil present, fugacious, or annuliform; cys-

tidia on the sides of the lamellae usually absent; spores medium to large; context bluing on exposure (reaching « deep Medici blue » Ridgway), and strongly reacting with monomethylparamidophenol.

Type species : P. cubensis (Earle) Sing.

P. cubensis (Earle) Sing. (Stropharia, Earle; Nematoloma caerulescens Pat.; Hypholoma, Sacc.; Stropharia, Sing.; Stropharia caerulescens Imai; Stropharia venenosa Imai; Stropharia cyanescens Murr.); obviously also *P. cyanescens* Wakefield apud Wakefield & Dennis and *P. caerulescens* Murr.

Sect. 3. ATROBRUNNEAE Sing. (1948). Pileus campanulate or conic at first, hygrophanous; stipe with fibrillose velutinous coating, or sometimes glabrous, exannulate; veil little developed and always absent in mature specimens; pleurocystidia few or numerous; on mud in swamps, among *Sphagnum*, on small sticks, on peat, never on dung.

P. atrobrunnea (Lasch) Gillet.

Sect. 4. TENACES (Fr.) Sacc., em. Pileus cylindric fusoid-campanulate acute, or convex becoming applanate, slightly viscid and subhygrophanous or partly hygrophanous, not very strongly hygrophanous, often with fulvous ocher or olive tinge and somewhat reminiscent in the general habit of the Naematolomas of the section *Psilocyboides*; veil very little developed, in some individuals practically absent, in others fibrillose subcortinoid and leaving indistinct traces in young specimens but never annuliform; pleurocystidia none; habitat on mud in swamps, among *Sphagnum*, on peat, on sticks and decayed trunks, also on the earth in low clearings, margins of the woods and in open coniferous woods, not on dung.

Type species : P. semilanceata (Fr.) Quél.

P. semilanceata (Fr.) Quél.

It is possible that *P. uda* (Pers. ex Fr. sensu Quél., Ricken) Gillet enters this genus but the author has not recently studied the cystidia.

KEY TO THE SPECIES

The small number of species admitted and the large number of species described, do not make it appear advisable to publish a key to the species of *Psilocybe* at the moment.

114. DECONICA (W. G. Smith) Karst.

Hattsv. Bidr. Finl. Nat. Folk **32** : xxvi. 1879

Type species : D. atrorufa (Schaeff. ex Fr.) Karst

Syn : *Agaricus* subgenus *Deconica* W. G. Smith, *Clavis Agaric.*, p. 23. 1870
Delitescor Earle, *Bull. N. Y. Bot. Gard.* **5** : 431. 1909

Characters : Pileus bay or date brown, tawny cinnamon, etc. in most species known at present, with usually striate margin when fresh and moist, strongly hygrophanous, becoming much paler when dry, with or without some floccons over the marginal part of the pileus or all over the surface of the pileus; this veil usually whitish and superficial, more rarely colored and more intimately attached (and then consisting of irregularly interwoven inequal hyphal elements, some of them rather short), or hanging from the margin (appendiculate); in some species a veil is seen in many individuals while in many others even the youngest carpophores are completely naked; epicutis proper consisting of hyaline, filamentous repent hyphae which are loosely arranged (subgelatinized in many species); hypodermium more irregular and consisting of larger elements but not distinctly subcellular, pigmented with a membrana pigment; hymenophore lamellate; lamellae very broad, usually broadly adnate to somewhat decurrent, slightly to strongly white fringed from the massed cheilocystidia which make the edge of the lamellae heteromorphous; spore print deep lilac or purplish fuscous to fuscous-sepia; spores sometimes lilac under the microscope if fresh (not dehydrated) and in H_2O medium (not in alkaline medium), more olive fuscous in KOH, and usually brownish melleous in NH_4OH, smooth, comparatively broad when seen frontally because of their lentiform shape, compressed both from the inner and outer surface (not from the sides) and about 0.7-1.3 μ narrower in profile (i. e. when the hilar appendage is turned obliquely to the right or left of the geometric basis), with thick, compound wall (with a distinct epi- and endosporium) which is interrupted by a broad truncate germ pore at the apex, usually smaller than 9 μ, more rarely reaching 11 μ in length (Pl. XI, 4); cystidia on the sides of the lamellae none; hymenophoral trama regular to subregular, becoming somewhat irregular in age in many species; stipe definitely centrally attached, longer than the diameter of the pileus, straight or somewhat flexuous but never strongly curved and always quite free from the

margin of the pileus, rather thin, with or without slight traces of the veil, which is rarely subannuliform, colored inside or at least at the base; context often hygrophanous, thin in the pileus except under the umbo in the larger umbonate species; hyphae nonamyloid, with clamp connections. On various substrata, mainly fallen leaves from trees and herbaceous plants, often on grasses, palms, ferns, among mosses, especially *Sphagnum* and *Polytrichum*, also on decaying wood, more rarely on peat, humus, dung, rotting nuts, etc.

Development of the carpophores : Pobably always hemiangiocarpous.

Area : Cosmopolitan, from the arctic to the tropics and from sea-level to the alpine zone.

Limits : *Deconica* differs from *Stropharia*, even if annulate, in having non-gelatinized surface of the stipe, smaller spores and darker pigments, and in never having any true pleurocystidia or chrysocystidia. It differs from *Psilocybe* in the characters indicated under the latter genus. It differs from *Kuehneromyces* in the more lentiform spores and the deeper colored spore print.

State of knowledge : It is at present impossible to tell the number of species belonging in *Deconica*, not even approximately. The author has recognized seven species as well known and with certainty belonging to *Deconica*. A monographic study would be very welcome.

Practical importance : None.

SPECIES

D. atrorufa (Schaeff ex Fr.) Karst. (Psilocybe, Quél.); *D. crobula* (Fr.) Romagnesi (Tubaria, Karst.; Naucoria, Ricken); *D. inquilina* (Fr.) Romagnesi (sensu Lange) (Tubaria, Gillet; Naucoria, Ricken; Psilocybe, Bres.; Melanotus, R. Maire); *D. physaloides* (Bull. ex Fr.) Karst. (non sensu Bres.) (Psilocybe, Quél.); *D. rhombispora* (Britz.) Sing. (Psilocybe, Sacc.; Stropharia rhombispora Hoehn.); *D. palmigena* (Berk. & Curt.) Sing. (Psilocybe, Sacc.); *D. bullacea* (Bull. ex Fr.) Karst. (sensu Ricken) (Psilocybe, Ricken).

KEY TO THE SPECIES

In view of what was said about the state of knowledge on the genus *Deconica*, a key cannot be given at present. The existing keys are insufficient. More importance must be attributed to the shape and size of the cheilocystidia and to the habitat which seems to be quite characteristic for some species.

115. MELANOTUS Pat.

Essai tax., p. 175. 1900.

Type species : *M. bambusinus* Pat.

Characters : Pileus brown, brown red, often almost whitish when dry, cuticle as in *Deconica ;* lamellae adnate; spores as in *Deconica* but less lentiform or not lentiform at all, never over 9 µ long; cystidia none on the sides of the lamellae but cheilocystidia numerous, making the edge of the lamellae heteromorphous: hymenophoral trama as in *Deconica*; stipe always shorter than the diameter of the pileus, always curved, usually eccentric and often attached to the margin of the pileus, at times strongly reduced and almost absent; context made up of nonamyloid hyphae with clamp connections and thin walls, non-gelatinized. On decaying plant debris, wood, and fabrics.

Development of the carpophores : Unknown.

Area : Most species limited to the warmer regions of the earth, especially the subtropics and tropics; however there are one or two species which are rarely found in the temperate zones of Europe and North America.

Limits : This genus is closest to *Deconica* and *Pleuroflammula.* Both differ in important characters which are easy to ascertain on fresh material, even without microscopical analysis.

State of knowledge : The genus as such is easily recognizable, but the determination of the species is extremely difficult. The species are arranged according to the host because this will make a tentative identification easier, but just what rôle the host plays in the intrageneric taxonomy of the *Melanoti* cannot be stated with certainty. The author admits ten species but it is possible that the number of the species in considerably lower than this since the morphological differences between these species are rather small.

Practical importance : One species (probably *M. musaecola*) is an active destroyer of fabrics in the tropics (Pl. V). It has been reported as such under the erroneous name *Claudopus variabilis (Mycologia* 38 : 677. 1946). The fungus has been seen by the author, and belongs undoubtedly in *Melanotus.*

SPECIES

On wooden boards, trunks and stumps:

M. proteus (Kalchbrenner) Sing. [Claudopus, (Kalchbr.) Sacc., on manufactured wood in South Africa]; *M. flavolivens* (Berk. & Curt.) Sing. [Crepidotus, (B. & C.) Sacc. on dead wood on Bonin Isls.]; *M. fumosifolius* (Murr.) Sing. (Crepidotus, Murr., on a dead log on Jamaica, W. I.); *M. haematites* (Berk. & Curt.) Sing. [Crepidotus, (B. & C.) Sacc., on dead wood in Hong Kong]; *M. Psychotriae* (Pat.) Sing. (Crepidotus, Pat., on *Psychotria glabrata*); *M. subvariabilis* (Speg.) Sing. (Claudopus, Speg., on « rotting branches » in Brazil).

On bamboo:

M. bambusinus Pat.

On dead trash and leaves of *Musa*:

M. musaecola (Berk. & Curt.) Sing. (Crepidotus, Sacc.).

On decaying coconut husks, and other palm débris:

M. subcuneiformis (Murr.) Sing. (Crepidotus, Murr.).

On dead herbaceous stems, including grasses, and on the spadix of *Zea*, etc.:

M. eccentricus (Murr.) Sing. (Crepidotus, Murr., on dead herbaceous stems in Jamaica, W. I.).

KEY TO THE SPECIES

The arrangement according to host plants is the best that can at present be offered to facilitate the identification of species in *Melanotus*.

Subfamily **Pholiotoideae** Sing.

Ann. Mycol **34**: 341 1936 (ut subfam Cortinariacearum), em

Type genus : Pholiota (Fr.) Quél.

Syn., *Pholiotoideae* Imai, *Journ Fac. Agr Hokk Imp Univ.* **43** (2) 179. 1938 (ut subfam. *Agaricacearum*).

Pholioteae Fayod, *Ann. Sc. Nat Bot.* VII. **9**: 360. 1889 (ut tribus Pholiotés), Romagnesi, *Rev. Mycol* **2**: 23. 1937 (ut tribus *Pholioteae*, nom. nud.); Imai, l. c. (ut tribus *Pholioteae*).

Characters : See key, p. 498.

KEY TO THE GENERA

A. Pileus squamose, or chrysocystidia present, pileus neither truly hygrophanous nor eccentrically stipitate nor sessile. 116. *Pholiota*

A. Pileus not squamose; chrysocystidia usually absent; pileus hygrophanous or stipe eccentric to completely reduced.

B. Stipe central or nearly so, longer than the average diameter of the pileus which is strongly and entirely hygrophanous; germ pore distinct and truncate; spore wall melleous. 117. *Kuehneromyces*

B. Stipe eccentric, at least in mature carpophores, shorter than the average diameter of the pileus, often strongly curved; pileus non-hygrophanous to somewhat hygrophanous; germ pore indistinct to distinct but rarely truncate; spore wall melleous or more intensely colored. 118. *Pleuroflammula*

116. PHOLIOTA (Fr.) Quél.

Champ. Jura Vosges, p. 124. 1872-73, em.

Type species : *P. squarrosa* (Pers. ex Fr.) Quél.

Syn. : *Agaricus* tribus *Pholiota* Fr., *Syst. Mycol.* 1 : 240. 1821.
Agaricus tribus *Flammula* Fr., *Syst. Mycol.* 1 : 250. 1821.
Flammula (Fr.) Quél. *Champ. Jura Vosg.*, p. 129. 1872-73, non D C. (1818).
Dryophila Quél., *Enchiridion*, p. 66. 1886.
Flammopsis Fayod, *Ann. Sc. Nat. Bot.* VII. 9 : 356. 1889.
Visculus Earle, *Bull. N. Y. Bot. Gard.* 5 : 437. 1909.
Hypodendrum Paul. ex Earle, *Bull. N. Y. Bot. Gard.* 5 : 445. 1909.

Characters : Pileus squamose (in subgenera *Hemipholiota* and *Eu-Pholiota*), or naked, viscid or dry, non-hygrophanous; lamellae variously attached, often sinuate or adnexed; hymenophoral trama regular in young carpophores; spore print frequently with a distinct rusty hue but not as brightly rusty colored as in *Conocybe* or *Gymnopilus*, somewhat variable in tinge but never purplish fuscous or lilac colored; spores under the microscope melleous to yellowish brown (NH_4OH), rarely fuscous in KOH; smooth, ellipsoid-oblong or ellipsoid fusoid to short-ellipsoid, smooth, with germ pore which is narrow and often indistinct; chrysocystidia present or in some of the scaly forms absent; cheilocystidia always present; stipe squamose or naked, dry or viscid, central; veil often appendiculate or annuliform, or both; context often bitter, hyphae often stained in the preparations by an intercellular bright yellow pigment soluble in

NH_4OH, always with numerous clamp connections. On wood (living and dead trees), on débris in the forest, in deep moss, on needles and foliage, on the earth in and more rarely outside the woods, on grass roots, on charcoal, etc.

Development of the carpophores. Hemiangiocarpous.

Area: Most species are definitely limited to the temperate zones, others reach the tropics or subtropics where the genus is poorly represented.

Limits. All authors, thus far, have followed Fries in separating the genus *Pholiota* from *Flammula*. Aside from the fact that *Flammula* is an homonym — which could be remedied by conserving the name for the fungus genus —, the genus *Flammula* is not tenable on taxonomic grounds. The characters indicated by the authors do not seem to hold when tested in the field and laboratory. The veil is often not annulate in certain species of *Pholiota*, and it is often annulate in species which according to their other characters are very closely related to forms considered as *Flammula* by the Friesian school. The author has attempted to separate the genus *Flammula* from *Pholiota* by emphasizing the absence of scales on the pileus and stipe of *Flammula*, and their presence in *Pholiota* sensu str. but it is to be doubted very strongly whether this character can successfully be used on the generic level. This opinion was first published by Singer & Smith, *Mycologia* 38: 264. 1946, and the two genera are consequently combined into one in the present work.

Pholiota in the larger sense, such as it is treated here, differs from *Kuehneromyces* plainly in the presence of chrysocystidia, or else in the completely different spores, the fleshier non hygrophanous, often squamose pileus, appearance and biology. *Pleuroflammula* is decidedly different in the pleurotoid habit and the small size correlated with the absence of chrysocystidia (except for one species where they are confined to the edge of the lamellae); in addition, the geographic area of the two genera is very different, *Pleuroflammula* being a predominantly tropical and subtropical genus, and *Pholiota* a predominantly temperate genus.

There is more difficulty in separating some forms with atypical spore color from the genera of the *Stropharioideae* than there is distinguishing the three genera of the *Pholiotoideae* from each other. This difficulty is especially apparent in the subgenus *Pseudonematoloma* where certain species would undoubtedly be inserted if it were not known from the literature that their spore print has the color of

that of the *Stropharioideae* rather than that of the *Pholiotoideae*. For further comment see p. 517, and under *Stropharia*, p. 500.

Concerning the separation of *Pholiota* from *Phaeomarasmius*, see under the latter genus.

State of knowledge: The knowledge of the species of *Pholiota* in the larger sense, and their taxonomy is comparatively good. However, considering the large number of species not fully known, and the practical importance of many Pholiotas in forestry, agriculture, as edible mushrooms, etc., it would be desirable to have more monographic work available. The author recognizes at present 30 species in this genus. Comparing this figure with the larger figure in Saccardo, one must take into consideration that the majority of the temperate Flammulas have been incorporated in *Pholiota*, and, at the same time, many elements of *Pholiota* in the original sense have been eliminated by transfer to other genera. At the same time, a limited number of Naucorias has been transferred to *Pholiota*, and a number of species has been disregarded in the enumeration because of the lack of vital information on them.

Practical importance: P. destruens, P. aurivella (sepecially *f. Abietis-Nordmannianae*), and *P. squarrosoadiposa* are very frequently active parasites and wood destroyers. They destroy trees in our forests as well as introduced park trees, and the mycelium continues its destruction after the tree is cut. Wooden bridges and similar wooden structures often deteriorate rapidly because of the action of certain basidiomycetes, among them Pholiotas. Few Pholiotas are edible, and even those are not widely known and little used. The only species with some market value is *P. nameko* (T. Ito) T. Ito & Imai, from Japan, but the author has not seen specimens of this species, and it may or may not belong in *Pholiota* as outlined here.

SPECIES

Subgenus **Hemipholiota** Sing. Pleurocystidia none, or rare and scattered and then not belonging to the chrysocystidia-type and not incrusted by a yellow to rusty melleous resinous incrustation.

Type species: P. destruens (Brond.) Quel.

Sect. 1. DESTRUENTES Konr. & Maubl. (1948). Pileus almost dry; spores with rounded apex.

Type species: P. destruens (Brond.) Quel.

P. destruens (Brond.) Quél., and perhaps also *P. heteroclita* (Fr.)

Quél. (which is said to be identical with *P. destruens* by Bresadola — in fact his *P. heteroclita* is identical with what is considered by the author as typical *P. destruens* — but is being distinguished by Lange and his school).

Sect. 2. **ALBOCRENULATAE** Sing. ined. Pileus more or less viscid; spores with subacute apex.

P. albocrenulata (Peck) Sacc. (Hebeloma, Sing.; Pholiota fusca Quél.)

Subgenus II. **Eupholiota** Lange (1938), em. (sensu str.) (genus *Hypodendrum* sensu Overholts 1932; sect. *Squarrosae* Konr. & Maubl. 1924-37; genus *Dryophila* Quél. subgenus *Pholiota* Quél. p. p.). Pleurocystidia rare to abundant, with strongly refringent amorphous body in the widest portion, this body yellow in ammonia and the whole interior of the cystidia often becoming blue in cresyl blue, often also somewhat incrusted by a yellowish to deep melleous-rusty resinous incrustation, always rather conspicuous; pileus squamose or squarrose, or squamulose; stipe also often squamose, often with an annulus which, however, is frequently indistinct or inconstant; spores of various sizes. Usually growing on wood, even on living trees, very few species on the ground.

Type species: P. squarrosa (Pers. ex Fr.) Quél.

Sect. 3. **SICCAE** Lange (1938, ut subsectio). Pileus non viscid.

Type species: P. squarrosa (Pers. ex Fr.) Quél.

P. flammans (Fr.) Quél.; *P. tuberculosa* (Schaeff. ex Fr.) Gillet; *P. curvipes* (Fr.) Quél.; *P. Maackiae* Sing.; *P. squarrosa* (Pers. ex Fr.) Quél.

Sect. 4. **ADIPOSAE** Konr. & Maubl. (1848) (= *Viscidae* Lange (1938, ut subsectio). Pileus viscid.

Type species: P. adiposa (Fr.) Quél. sensu Ricken, Lange, Konr. & Maubl. non aut. Americanorum.

P. squarrosoides (Peck) Sacc.; *P. squarrosoadiposa* Lange (P. intermedia Lange non Sing. nec A. H. Smith); *P. aurivella* (Batsch ex Fr.) Quél.; *P. lucifera* (Lasch) Quél.; *P. adiposa* (Fr.) Quél. sensu Ricken, Lange, Konr. & Maubl. non aut. Amer.

Subgenus III. **Flammula** (Fr. 1821 ex Fr. 1874, ut subgenus *Agarici*) Sing. 1948 [Genus *Visculus* Earle; genus *Flammula* (Fr.) Quél. max. e parte; *Flammula* subgen. *Eu-Flammula* Sing. 1937, Lange 1939; genus *Dryophila* Quél. subgen. *Flammula* (Fr.) Quél. 1886 (maxima e parte)]. Cystidia as in subgenus *EuPholiota*; pileus glabrous or at least naked, or becoming so after the velar floccons have

been lost in the maturing carpophore; stipe also not squamose except from the veil, and not viscid; spores usually small (up to 10.5 μ); habit as in *Stropharia*, *Naematoloma* sect. *Flammuloides*, *Pholiota* subgenus *EuPholiota*, i. e. stipe not exceedingly elongate in an average and pileus rather fleshy; annulus either present, or absent, and then the marginal veil often appendiculate and strongly developed as in certain species of *Naematoloma*. On the earth, on decaying wood, on charcoal, rarely in wounds and around the base of living trees, on grass roots, and on various débris.

Type species: Flammula flavida (Schaeff. ex Fr.) Quél.

Sect. 5. UDAE (Fr. ut sectio *Agarici*, trib. *Flammula*) Sing. em. Cuticle of the pileus humid or dry, non viscid or sometimes subviscid after prolonged rains, never truly viscid or glutinous and not easily separable from the context of the pileus; veil usually scantily developed and mostly clinging to the margin of the pileus, rarely annuliform (in *P. duroides*); spore print rusty fuscous.

Type species: Flammula flavida (Schaeff. ex Fr.) Quél.

P. duroides *Peck* (Flammula, Sing.); *P. flavida* (Schaeff. ex Fr.) Sing. (Flammula, Quél.); *P. fusa* (Batsch ex Fr. sensu Ricken) Sing. (Flammula, Gillet); *P. semiimbricata* (Sing.) Sing. (Flammula, Sing.); *P. graminis* (Quél.) Sing. (Flammula, Sing. 1940); *P. abstrusa* (Fr. sensu Lange) Sing. (Flammula, Romagnesi; Naucoria, Sacc.); *P. astragalina* (Fr.) Sing. (Flammula, Quél.). *P. alnicola* (Fr.) Sing. (Flammula, Quél.); *P. pseudofascicularis* Speg. [Flammula alnicola var. salicicola (Fr.) Sacc.].

Sect. 6. LUBRICAE (Fr. ut sectio *Agarici* trib. *Flammula*) Sing. Pileus with a lubricous, glutinous, truly viscid pellicle, often with evanescent white or colored squamulae from the abundantly developed veil; spore print without a distinct rusty tinge in most species.

Type species: Flammula lubrica (Pers. ex Fr.) Quél.

Subsection Polychroinae Sing. (1948). Pileus cinnamon fulvous, brown, pink, red, green, vinaceous purplish, pallid, clay color, or with several of these colors mixed, or variable within this color range; stipe in some species partly pallid to pure white in youth; young lamellae whitish to purplish argillaceous, not yellowish; veil strongly developed; spores small; spore print from «tawny olive» to «sepia» (Ridgway), or nearly so.

Type species: *P. polychroa* (Berk.) A. H. Smith & Brodie.

P. Freindlingiae (Sing.) Sing. (Flammula, Sing. 1936); *P. lenta* (Pers. ex Fr.) Sing. (Flammula, Gillet); *P. lubrica* (Pers. ex Fr.) Sing.

(Flammula, Quél.); *P. polychroa* (Berk.) A. H. Smith & Brodie (Flammula, Sacc.); *P. appendiculata* Peck.

Subsection **Spumosinae** Sing. (1948) Pileus pale yellowish green to bright lemon yellow or brownish yellow near the margin and more fulvous-tawny rusty in the center in many specimens or species, or eventually almost entirely colored rusty brown; stipe not white, not even in part when young; lamellae yellowish in youth; veil usually not very strongly developed (not annular, and not leaving conspicuous floccons on the surface of the pileus except for the very margin); spores small to medium sized (5.5-10.5 μ); spore print tabacco brown, i. e. « burnt umber » (Maerz & Paul), or from « snuff brown » to « Prout's brown » (in *P. carbonaria*) of Ridgway.

Type species : P. spumosa (Fr.) Sing.

P. spumosa (Fr.) Sing. (Flammula, Karst.); *P. bicolor* (Speg.) Sing. (Flammula, Speg.) *P. gummosa* (Lasch) Sing. [Flammula, Quél.; Flammula ochrochlora (Fr.) Sacc.]; *P. carbonaria* (Fr.) Sing. (Flammula, Quél. — by some considered to be a variety of *P. spumosa*).

Subgenus IV. **Phaeonematoloma** Sing. (1937) (ut subgenus generis *Flammulae*). Pileus more or less viscid; stipe either dry or viscid from a viscid veil, rather elongate in most species, especially those growing in *Sphagnum*, and then assuming the external appearance of *Naematoloma* sect. *Psilocyboides*; veil always manifest, in some species appendiculate, in others annulate; spores always larger than 10.5 μ or at least a large percentage of the spores of a print larger than 10.5 μ.

Type species . Flammula myosotis (Fr.) Sing.

P. myosotis (Fr.) Sing. (Naucoria, Quél.; Flammula, Sing. 1937); *P. lapponica* (Fr.) Sing. (Naucoria, Sacc.; Flammula, Sing. 1937); probably or possibly belonging here: *Stropharia semigloboides* Murr.; *Hypholoma anomalum* A. H. Smith; *Hypholoma viscidipes* A. H. Smith.; *Flammula malicola* Kauffm. (Pholiota malicola A. H. Smith); *Stropharia silvatica* A. H. Smith; *Flammula mixta* (Fr. sensu Ricken) Sacc.; and *Naucoria scorpioides* (Fr.) Karst.

Note : A specimen of *Stropharia semigloboides* collected by A. H. Smith is microscopically a true representative of this genus, yet, the spore print of specimens collected more recently, is according to A. H. Smith's oral communication, « purple », meaning the color of the spore print as observed in the *Stropharioideae*. The opposite is true as far as *P. malicola* is concerned where the spores are typically

seen under the microscope in KOH mounts, yet the spore print fits *Pholiota*. It appears that on the level of *Phaeonematoloma* and *Naematoloma*, the spore print becomes unreliable as the sole distinguishing character. Consequently, the author believes that in a future delimitation of these two groups other characters (perhaps the viscidity of the stipe, etc.) must be considered in order to determine the generic position of a given species. Only a monographic study will eventually succeed in establishing a thoroughly sound delimitation. The microscopical characters used in the *Stropharioideae* in order to delimit *Naematoloma* cannot be used for this particular purpose since the lamellae have persistently regular trama and the hypodermium is subcellular in both *Naematoloma* and *Phaeonematoloma*. In both *Naematoloma elongatipes* and *Pholiota myosotis* the spore print is « cocoa » (Maerz & Paul), i. e. very slightly more purplish than in the *Pholiotae* in general. Consequently the whole subgenus might be transferred to *Naematoloma* as suggested by A. H. Smith (Mycologia **42**: 322. 1950)

117. KUEHNEROMYCES Sing. & Smith

Mycologia **38**: 504. 1946

Characters: Pileus glabrous, naked, opimous to subviscid but not glutinous, hygrophanous all over, margin transparently striate in moist condition, cinnamon brownish, or some shade close to it, perhaps also more yellow, olive or red; epicutis consisting of subparallel, thin filamentous, repent, hyaline, subgelatinized clamped hyphae; hypodermium consisting of irregular, rather broad, eventually often thick-walled hyphae; dermatocystidia none; lamellae variously attached, never free; spore print cinnamon or brown (between 176 and 191 of Séguy, or between « Verona brown » and « cinnamon brown » or near « snuff brown » or « Brussels brown » of Ridgway, or plate 15, E 12 of Maerz. & Paul); spores under the microscope melleous, with double wall, the endosporium pallid and about as thick as the episporium, smooth, rather small, ovoid to ellipsoid, not or only very slightly lentiform, truncate at the apex, with a distinct and constant germ pore (Pl. XXIII, B, 2); basidia normal in all regards, cheilocystidia present, but sometimes two types of cheilocystidia present (Pl. XXIII, B, 7), and sometimes only one type (Pl. XXIII, B, 1, 3, 6), and then cheilocystidia scattered to crowded (making the edge of the lamellae heteromorphous);

chrysocystidia and generally all kinds of pleurocystidia mostly absent; trama regular; stipe centrally attached except in aberrant carpophores very rarely observed, long (i.e. much longer than the diameter of the pileus), straight or flexuous, or slightly curved if growing from a vertical surface, stuffed, eventually hollow, scaly or naked; veil present, and sometimes annuliform, sometimes extremely fugacious; context consisting of hyphae with clamp connections. On wood, sawdust, often precocious.

Development of the carpophores: Hemiangiocarpous.

Area: In the temperate zone but reaching the subtropical and tropical zone occasionally, in the palaeotropics only in high elevations (Java), most common in the northern part of North America and in Siberia.

Limits: *Kuehneromyces* differs from the related genera in the characters emphasized in the key. Among the Pholiotas it comes closest to the subgenus *Hemipholiota*, but differs in broader germ pore and hygrophanous pileus.

State of knowledge: This genus has been monographed by Singer & Smith (*Mycologia*, **38**: 500-523. 1946). Six species are known at present.

Practical importance: Probably all species are edible; the one most widely used is *K. mutabilis*. Only the pilei are used for food; the stipes are discarded. *K. mutabilis* frequently occurs on structural timber, such as wooden bridges, but it does not destroy healthy wood; when if forms carpophores on wood, the wood is usually already strongly decomposed. It was found to cause a strong red-brown pulp rot on *Picea* in Norway (see *Friesia* **1**: 91. 1933).

SPECIES

K. mutabilis (Schaeff. ex Fr.) Sing. & Sm. (Pholiota, Quél.); ***K. rostratus*** Sing. & Sm.; ***K. depauperatus*** Sing. & Sm.; ***K. vernalis*** (Peck) Sing. & Sm. [Naucoria, Sacc.; Naucoria praecox Murr.; Pholiota marginella Peck; Naucoria lignicola (Peck) Sacc.]; also ***K. rhaicolor*** (Pat.) Sing. [Flammula, Pat. and Flammula chrysopellus (Berk. & Curt.) Sacc. sensu Pat. non al., non B & C.]; also ***K. nudus*** Sing.

KEY TO THE SPECIES

The author refers the reader to the paper by Singer & Smith (l. c.) which contains a key (p. 504).

118. PLEUROFLAMMULA Sing. apud Sing. & Sm.

Mycologia 38 : 521. 1946.

Type species : *P. Dussii* (Pat.) Sing.

Characters : Pileus yellowish to rich chestnut brown, often both colors present, fibrillose subtomentose to glabrous, non viscid, non-hygrophanous to subhygrophanous, small; epicutis consisting of repent hyphae with or without pigment incrustations or at least with membrana-pigment, some of the terminal members of the epicuticular hyphae at times assuming the shape of dermatocystidia but very scattered; spore print rusty brown; spores a rich deep rust color or rusty-ochraceous when seen under the microscope, smooth, with distinctly double (episporium and endosporium) wall, very broadly rounded below with the hilar end little marked, the apex with a very indistinct to distinct germ pore but rarely truncate and even then only indistinctly so, small to moderately large (Pl. XXIII, B, 5); hyphae of the young hymenophoral trama regular with very thin walled hyphae; cheilocystidia (Pl. XXIII, B, 4) always present and very conspicuous, hyaline, very rarely a few cheilocystidia assuming the character of chrysocystidia; pleurocystidia none; stipe — if present — very short (shorter than the diameter of the pileus), curved in all specimens and often touching the margin of the pileus, eccentric to almost lateral; veil present (or sometimes absent ?); context consisting of a fleshy trama; hyphae with clamp connections; in some species, there is a bright and rich colored (yellow) pigment, probably of intercellular origin, that is easily dissolved in ammonia and finally dyes all the cells of the preparation containing it. On various frondose trees and shrubs, mostly on dry limbs and on fallen branches, logs, etc.

Development of the carpophores : Probably hemiangiocarpous.

Area : North, Central, and South America, in the temperate, subtropical, and tropical zone of both hemispheres, the northern as well as the southern; probably also in the eastern hemisphere.

Limits : This genus differs amply from all genera of this group. It also differs from the analogous genus *Melanotus* which has purplish fuscous or deep lilac spore print and lacks the yellow soluble pigment of many *Pleuroflammulae*. The cheilocystidia have another shape (mostly ampullaceous with slightly capitate apices) than most species of *Pleuroflammula* and are usually smaller than in the latter genus.

Pleuroflammula differs from *Crepidotus* with which it has hitherto been confused, in the presence, at least in most species, of a veil, and in the constant absence of gelatinized layers and presence of clamp connections; besides the exact colors of the spore prints are probably different in all species of *Crepidotus* but too few good spore prints have yet been studied in *Pleuroflammula*. *Pleuroflammula* also comes close, in external aspect, to some species of *Phaeomarasmius*. Microscopically, the structure of the cuticle of the pileus and the callate instead of pore-bearing spores which, in addition, are usually larger than those of *Pleuroflammula*, clearly separate *Phaeomarasmius* from *Pleuroflammula*.

State of knowledge: Six species are known at present.

Practical importance: None.

SPECIES

P. Dussii (Pat.) Sing. (Crepidotus, Pat.); *P. Bruchii* (Speg.) Sing. (Crepidotus, Speg.); *P. puberula* (Peck) Sing. (Crepidotus, Peck); *P. chocoruensis* Sing.; *P. flammea* (Murr.) Sing. (Crepidotus, Murr.); probably belonging here: *Crepidotus Phillipsii* (B. & Br.) Sacc.

KEY TO THE SPECIES

A. Pigment of the context and hymenophoral trama abundant, probably intercellular, soluble in ammonia to a rich yellow solution permeating the whole preparation. Species occurring in North America, eastern states.

B. Nearly all cheilocystidia capitate. Virginia to Florida. *P. flammea*

B. Cheilocystidia very variable in a single carpophore, very few capitate. New Hampshire. *P. chocoruensis*

A. Pigment of the context and the trama not abundant and not permeating the whole preparation. Western and extra North-American species.

C. Tropical species with ampullaceous cheilocystidia. Antilles. *P. Dussii*

C. Extra-tropical species; cheilocystidia only exceptionally ampullaceous.

D_1. Cheilocystidia often ventricose and 4.2-6.2 μ thick. California. *P. puberula*

D_2. Cheilocystidia mostly not ventricose, 3.7-5.8 μ thick; spores broader 8.8-9.8 × 6.3-7.3 μ. Argentina. *P. Bruchii*

D_3. Cheilocystidia clavate with filiform apiculus. Europe. (see *Crepidotus Phillipsii* (B. & Br.) Sacc.

GENERA IMPERFECTLY KNOWN

Gymnocybe Karst., *Hattsvampar*, *Bidr. Finl. Nat. Folk* 32: xxvii. 1879. « Differs from *Flammula* (Fr.) by the lack of a veil. Analogous

to *Clitocybe* and *Clitopilus*» Karsten. The lectotype is *Gymnocybe Weinmannii* (Fr.) Karst. This a dubious species; therefore, the genus is dubious also, particularly since it appears improbable that the type of the species can be found and restudied.

Phleboncma Heim, *Compt. r. Acad. fr.* **188**: 1567, 1929. «Carpophore fleshy, not hygrophanous, with initially incurved margin, with ... glabrous, non-viscid cuticle; stipe not separable from the pileus, solid; lamellae completely free, numerous, broad; flesh white, intensely staining yellow when bruised, formed by hyphae which are all more or less vascular; spores (in mass) pale ocher, (under the microscope) small (5-5.6 × 4-4.5 μ in the type species), smooth, subtetragonal in outline, with a large suprahilar applanation, without germ pore, with distinct and small hilar appendage; basidia clavate-elongate, tetrasporous; cystidia none, edge of the lamellae homomorphous; on the earth.» Heim. The type species is *Phleboncma chrysotingens* Heim, a species described by Heim from Madagascar. It has a cutis on the pileus, consisting of filamentous hyphae which are illustrated in «*Le Genre Inocybe*», Paris 1931, p. 60, fig. 98, A. Here, the septa are drawn clampless; the spores are said to consist of a hyaline episporium and brown endosporium (which is rather unusual). The context consists entirely of conducting elements (l. c., fig. 98 C), and toward the cuticle more and more ordinary hyphae are intermixed (fig. 98 B).

The author has not seen the type, but it seems rather obvious that this species has no close relatives in the *Strophariaceae*, or for that matter in any ochrosporous group. The description impresses one as suggesting a species of the family *Agaricaceae* (sensu nostro), and it would be interesting to check on the behavior of the spores of *Phleboncma* in cresyl blue, in the Melzer reagent, etc.

CORTINARIACEAE Roze

Bull. Soc. Bot. Fr. **23**: 51. 1876 (ut Cortinariées, nom. nud.), diad., p. 113; Heim, *Treb. Mus. Cienc. Nat. Barcelona* **15**: 115. 1934

Type genus: Cortinarius Fr.

Syn. *Cortinariaceae* subfam. *Cortinarioideae* Sing., *Ann. Mycol.* **34**: 341. 1936.
Cortinariaceae subfam. *Galerinoideae* Sing., *Ann. Mycol.* **34**: 342. 1936.
Agaricaceae trib. *Cortinarieae* Fayod (1889), Konr. & Maubl. (1924-37), (both as *Cortinariés*), Imai (1938): *Inocybes, Naucoriés* (p. p.) Fayod 1889,
Eu-Derminaceae Romagnesi, *Rev. Mycol.* **2**: 182. 1937 (nom. nud.), p. p.
Phaeolaceae Romagnesi, *Rev. Mycol.* **2**: 178. 1937 (nom. nud.), p. p.

Characters: Structure of the epicutis varying from genus to genus but rarely cellular as in the *Bolbitiaceae* (though sometimes an epithelium in certain species of *Naucoria*) but most frequently either a trichodermium with dermatocystidioid terminal members, or a cutis; hymenophore lamellate; hymenophoral trama definitely regular; spore print brownish argillaceous to bright and rich ferruginous-fulvous; spores always with compound wall (endosporium and episporium, often ornamented, warty from a probably exosporial layer, and with a sometimes rather persistent perisporium), without germ pore, but often with a callus; basidia quite normal in all regards; cystidia often present, more frequently on the edges of the lamellae, more rarely on the sides of the lamellae, and in many species of *Cortinarius* and also in *Rozites* neither with cheilocystidia nor with pleurocystidia; stipe central, more rarely eccentric, lateral or absent; veil present, or absent; context with clamp connections, more rarely without them (one species of *Alnicola* and one section of *Galerina*). On the earth in woods, more rarely on wood, on grass roots, stems, rhizomes of orchids, ferns, on palm leaves, foliage of various plants, charcoal, and in deep moss.

Limits: The *Cortinariaceae* « touch » the *Strophariaceae* on one side, and the *Crepidotaceae* and *Paxillaceae* on the other. The *Strophariaceae* differ from the *Cortinariaceae* in the presence of a germ pore in the spores — however poorly developed — and or chrysocystidia on the sides of the lamellae. The *Crepidotaceae* differ in simpler spore wall structure as far as the different layers are concerned, and in often uninucleate spores. The *Paxillaceae* may also occasionally resemble the *Cortinariaceae*, especially the species with warty spores; they differ in having the hymenophoral trama never quite regular in the younger stages.

Phylogeny: The *Cortinariaceae* may have their origin in the *Strophariaceae* and thus link themselves to the group of families that is related to certain non-hypogaeous *Gastromycetes* with germ pore (*Agaricaceae*, *Coprinaceae*, *Bolbitiaceae*, *Strophariaceae*), or they may be closer to the genera with roughened spores in the *Crepidotaceae* and *Paxillaceae* whereby they would be linked with the group of families that tend toward the *Boletaceae* and the hypogaeous *Gastromycetes* with spores without germ pore. As a third possibility, one may mention a derivation of the *Cortinariaceae* directly from certain *Secotiaceae* with warty spores. The latest investigations of the author show that the latter hypothesis is by far the most probable.

Within the *Cortinariaceae*, there are two series, comparable to the *Strophariodeae* and *Pholiotoideae* in the *Strophariaceae*, also based on the color of the spore print, likewise showing an evolution along different lines in each of the series, and, just as in the *Strophariaceae*, difficult to distinguish on a certain level (*Naucoria*, *Phaeomarasmius*, etc.). Volvate forms occur in *Inocybe*, *Cortinarius* and *Rozites*. Since the author considers the volvate forms as primitive, these genera have been put at the beginning of their respective series which are called *Inocybeae* and *Cortinarieae*.

KEY TO THE TRIBUS

A Spore print brownish argillaceous or dirty ochraceous fuscous (for exact colors see under the genera Nº 119, 120, 122; spores often nodose subangular or even star shaped, or else smooth or warty rough, but never with plage; cheilocystidia always present, or else cystidia occurring on the edge. *Inocybeae*, p. 524.

A Spore print rusty brown to bright and rich ferruginous fulvous rarely ochraceous; spores never nodose-angular and never stellate; spores often with plage; cheilocystidia either present or absent *Cortinarieae*, p. 544

Tribus INOCYBEAE Fayod

Prodr., *Ann. Sc. Nat.*, *Bot.* VII, **9**: 361. 1889 (ut *Inocybes*)

Type genus: *Inocybe* (Fr.) Quél.

Syn.: *Naucorieae* Fayod, l. c., p. 357 p. p. (ut *Naucoriés*), Imai *Journ. Fac. Agr. Hokk. Imp. Univ.* **43** (2): 248. 1938, p. p.
Hebelomeae Romagnesi, *Rev. Mycol.* **2**: 178. 1937. nom. nud.

Characters: See key above.

KEY TO THE GENERA

A Pileus without dermatocystidia (or very rarely with scattered ones of the *Inocybe*-type, and then the pileus radially fibrillose), and without round cells on its surface; the cuticle is formed by a cutis or else by a trichodermium, or by remnants of either, macroscopically fibrillose to scaly-lacerate or smooth and then viscid.

B Pileus fibrillose, rarely viscid (and then pleurocystidia thick walled and/or spores nodulose subangular, or odor spermatic); if there are no pleurocystidia, the spores are usually phaseoliform; ornamentation of the spores never warty-rough (type III-IV-V-VII) 119 *Inocybe*

B Pileus viscid, and besides sometimes silky-fibrillose from the veil, rarely becoming dry because of the loss of the gelatinized epicutis; cheilocysti-

dia always present and making the edge of the lamellae heteromorphous, but true pleurocystidia absent (metuloids always absent); spores almond-shaped to ellipsoid-oblong or ellipsoid, warty-rough, rarely smooth 120. *Hebeloma*

A. Pileus with dermatocystidia (analogous to the cheilocystidia), or with vesiculose cells forming an epithelium or a palisade; cuticle definitely not consisting of an unorganized trichodermium or a cutis.

C. Spores distinctly warty. 121. *Alnicola*

C. Spores smooth

D. Not all sterile surfaces covered by an epithelium; pileus hygrophanous. 122. *Naucoria*

D. All sterile surfaces covered by an epithelium, or at least numerous spherocysts present on the surface of the pileus and on the stipe; pileus non hygrophanous, rarely hygrophanous

(see *Phaeomarasmius*, p. 573)

119. INOCYBE (Fr.) Fr.

Monographia Hym. Suec. **2**: 346. 1863.

Type species: *Agaricus trechisporus* Berk.

Syn.: *Agaricus* trib. *Inocybe* Fr., *Syst. Mycol.* **1**: 254. 1821.
Astrosporina Schröter in Cohn, *Kryptog. fl. Schlesien, Pilze*, p. 576. 1889.
Clypeus (Britz.) Fayod, *Ann. Sc. Nat.* VII **9**: 362. 1889.
Agaricus subgen. *Clypeus* Britz., *Hymen. Südb.* **3** *a*: 4. 1882 (com. nud.); **3** *b* (*Nat. Hist. Ver. Augsburg. Ber.* **27**: 149). 1883.
Agmocybe Earle, *Bull. N. Y. Bot. Gard.* **5**: 439. 1909.
Inocibium Earle, l. c., p. 440.

Characters: Pileus fibrillose, the fibrils arranged radially, often splitting radially and then characteristically rimose, or disintegrating and then irregularly lacerate, often also scaly or squamulose, and sometimes with a pallid fibrillose patch from the volva which is rarely developed enough to show up on the surface of the pileus, the uppermost layer of the pileus consisting of repent or at any rate not palisadic hyphae which are always elongate to filamentous and usually radially arranged, rarely imbedded in a gelatinous mass; dermatocystidia rarely present and then very scattered and about the same shape as those of the lamellae; lamellae adnexed to broadly adnate, often sinuate, usually whith paler edge when nearly mature; spore print about the same color [12] as in *Hebeloma* (see there), never distinct-

[12] E. gr. between « Cochin » and « burnt umber » (Maerz & Paul) in *I. relicina* (print 1 year old), and « Raw umber » in *I. lacera* (print fresh), also « Malay » in some species, or Pl. 15, 12 E in *I. geophylla*.

ly rusty, rarely almost pallid white (*I. cystidiosa*); spores smooth, i. e. not rough or warty, but sometimes nodose subangular (Pl. XIV, 2), or even stellate-spinose; phaseoliform reniform, or almond shaped, or subellipsoid elongate, or cylindric, with double wall, without germ pore; cystidia always present but in some species restricted to cheilocystidia which are then usually clavate-vesiculose, or else assuming the characters of metuloids, often with thick, somewhat stramineous walls and ampullaceous in many cases, rather large and very conspicuous, and in this case usually also occurring on the sides of the lamellae, the pedicel deep rooting, the apex often mucronate with amorphous (resinous) or crystalline incrustations (the cystidia of the latter type are «metuloids» or «cystidia of the *Inocybe*-type (Pl. XVII, 1); stipe central; often beset with dermatocystidia, mostly pruinose from the dermatocystidia at the apex, but in some species with dermatocystidia all the way downwards to the base, the extent of the cystidiate area depending on the attachment of the cortina to the stipe; the cortina often very abundant, in other cases scanty and fugacious, attached to the apex or to the upper portion of the stipe, or also attached to the base of the stipe and forming the continuation of the margin of a bulb (and in this case, the stipe usually pruinate cystidiate all over), fibrous fleshy or fleshy, rarely volvate; the partial veil (cortina) usually continuous with the cuticle of the pileus or adnate to it; context fleshy in the pileus, often with a strong characteristic odor (spermatic, aromatic-fruity, of truffles, of camphor, etc.); all hyphae with clamp connections.

Development of the carpophores: Hemiangiocarpous (according to Heim and Douglas).

Area: Cosmopolitan.

Limits: The limits of this genus are rather easy to draw, and, in fact, even the beginner will be capable of telling an *Inocybe* in the field after a short time of experience. If the microscopical characters are also taken into consideration, the identification of an *Inocybe* as such does not cause any difficulties. The nodulose spores of many Inocybes are unique in the agarics, and, for that matter in the *Agaricales* (only some *Thelephoraceae*, the genus *Cystoagaricus,* and the genus *Rhodophyllus* have comparable but not identical spores); the pleurocystidia, once seen, will also serve as a reliable means of identification where they are present. Even similar cystidia in other groups such as the cystidia of *Galerina nana* differ chemically from

mentally different. For example, the cystidia of the latter species though morphologically so similar to those of the Inocybes, have strongly metachromatic walls when studied in cresyl blue whereas the typical *Inocybe* cystidia have (excepting sometimes the very apex) non metachromatic walls, i. e. the walls are blue in cresyl blue. For more details see Kühner, *Bull. Soc. Mycol. Fr.* **50**: 76 77. 1934. This leaves only the group without true *Inocybe* cystidia and non nodulose spores which is also rather easily recognizable by the character of the covering of the pileus, and the shape of the cheilocystidia (clavate-vesiculose to saccate piriform). The pileus is never truly and persistently viscid in the species without pleurocystidia (in contrast to *Hebeloma, Naucoria* and *Agrocybe*), and the spores are usually phaseoliform reniform rather than almond shaped as in *Hebeloma*. If these characters are kept in mind, it is possible to distinguish the *Inocybes* in all cases from *Hebeloma*, even if the spores of the *Hebeloma* should be smooth (which is often the case in two spored forms of *Hebeloma* [122], or if the *Inocybe* should be viscid.

State of knowledge: The genus *Inocybe* has been studied very carefully by a number of authors both in Europe and America (Kauffman, Heim, Kühner & Boursier, Kühner, more recently also by A. H. Smith and by D. A. Stuntz), yet there seems to be an inexhaustible abundance in forms, something Fries has never dreamed of, and if Europe and North America furnish such a stunning number of forms, it is not surprising to find that other continents, especially Asia, are very little explored as to their *Inocybe* flora, yet rich in species. The number of species admitted by Heim is 64. The forms with nodose spores treated by Kühner, number 23. The total number of well known species in *Inocybe* exceeds 100.

Practical importance: Two Inocybes, *I. cutifracta* Petch (tropical Asia) and *I. jurana* Pat. (Europe) are reported to be edible. Several species cause more or less severe poisoning, especially *I. Patouillardii*. Many are reported to be mycorrhiza fungi with forest trees but this point has not yet been proved experimentally.

[122] Two-spored basidia are extremely rare in *Inocybe*, and restricted to only one group, the group of *I. hirtella*. In contrast to this, bisporous basidia are found commonly in *Galerula*, *Naucoria*, and *Hebeloma*.

SPECIES

The author reproduces here the classification given by R. Heim. This classification seems to express the phylogenetic tendencies in the genus, as they appear to show on the basis of the material known to Heim. On the other hand, his classification is somewhat more difficult for practical purposes than that used by Kauffman and by Kühner & Boursier. The author refers to Kauffman's treatment of *Inocybe* in *North American Flora* **10**: 227-260. 1924 which is easily available. Boursier & Kühner's and Kühner's work on the gonosporous (i. e. with nodulose-angular spores) Inocybes is more difficult to obtain and to use, and consequently, the author considered it desirable to compile the essential parts of their work as an alternative treatment.

No effort has been made on the part of the author to reconcile these treatments where they diverge, or to supplement Kühner's treatment by adding the data on the non gonosporous Inocybes. After more data on more species in more different geographic areas have been accumulated, a synthesis between these classifications will probably be possible. In the meantime, the best that can be done is to attempt a fair representation of the present status of our knowledge of the genus.

Heim's diagnoses of the subdivisions of this genus do not always clearly oppose the characters of the units in question. The author has at times added or omitted certain characters; Heim himself is not responsible for these changes, and the reader is referred to the original monograph: Heim, R. *Le Genre Inocybe, précédé d'une introduction générale à l'étude des Agarics Ochrosporés.* Paris. 1931. The type species of the sections are lectotypes proposed by the author.

Boursier & Kühner's, Kühner & Boursier's, and Kühner's papers on *Inocybe* have appeared in the *Bulletin de la Société Mycologique de France* **44**: 171. 1928; **48**: 118. 1932; **49**. 81. 1933.

I

COMPILATION FROM HEIM, L. C.

Sect. 1. VISCOSAE Heim (1931). Pileus generally viscid in fresh condition, then becoming sericeous fibrillose; lamellae cream ocher,

or camphoric, or none; context unchanging; excretive hyphae not abundant; spores ovoid or amygdaliform; guaiac solution negative with the flesh.

Type species: *I. viscidula* Heim.

Stirps **Viscidula** (Habit of *Hebeloma*).

I. viscidula Heim; *I. cucullata* Ch. Martin [43].

Stirps **Vatricosa** (Habit of *Naucoria*).

I. vatricosa (Fr.) Karst.; *I. trechispora* (Berk.) Karst.

Stirps **Geophylla** (Typical *Inocybe* habit).

I. geophylla (Sow. ex Fr.) Quél.; *I. umbratica* Quél., *I. sambucina* (Fr.) Quél.

Sect. 2. **DULCAMARAE** Heim (1931). Pileus dry, with abundantly fibrillose cuticle, generally with involute margin, bister to ochraceous brown; stipe usually tapering toward the base, with a covering which is identical with that of the pileus, almost always hollow; cortina abundant, persistent; lamellae often triangular; context ochraceous at least in the stipe, sometimes bluing in the base, rarely white, without odor, or with aromatic-fruity odor; excretive hyphae rarely abundant; spores not nodulose subangular; guaiac without any action.

Type species: *I. dulcamara* (A. & S. ex Fr.) Quél.

Stirps **Hystrix** (Muricate pleurocystidia present; carpophores not entirely unicolorous).

I. hystrix (Fr.) Karst.

Stirps **Hirsuta** (Muricate pleurocystidia none, carpophores not entirely unicolorous).

I. calamistrata (Fr.) Gillet; *I. hirsuta* (Lasch) Quél.; *I. relicina* (Fr.) Quél. sensu Heim.

Stirps **Dulcamara** (Pleurocystidia present or absent; the entire carpophore unicolorous).

I. dulcamara (A. & S. ex Fr.) Quél. sensu Ricken, p. p.; Heim; *I. Malenconii* Heim; *I. perbrevis* (Weinmann) Gillet sensu Cooke, Heim; *I. caesariata* (Fr.) Karst. sensu Heim; *I. carpta* (Scop. ex Fr.) Quél. sensu Heim.

Sect. 3. **RIMOSAE** (Fr.) Quél. (1872-73) em. Heim. Pileus fibril-

[43] This species is not indicated as being viscid in Heim's description. If it actually were viscid, it might also be considered as a transition toward *Hebeloma*. Having no personal experience with the species in question the author reserves

lose rimose, ocher or brown, not viscid; stipe, lamellae and context without lilac or violet color; lamellae not ventricose, olive or cinereous-brown; odor spermatic, rarely aromatic-fruity or of truffle; excretive hyphae rare, or sometimes abundant; spores ovoid phaseoliform, or phaseoliform ventricose or elongate; muricate pleurocystidia none; cheilocystidia claviform-oblong; guaiac mostly negative with the context.

Type species: I. fastigiata (Schaeff. ex Fr.) Quél.

Stirps **Fastigiata** (Schaeff. ex Fr.) Quel. (Odor spermatic). *I. fastigiata* (Schaeff. ex Fr.) Quel.; *I. squamata* Lange; *I. mimica* Mass.; *I. perlata* (Cooke) Sacc.

Stirps **Cookei** (Odor aromatic fruity).

I. Cookei Bres.

Stirps **Maculata** (Odor of truffles).

I. maculata Boud.

Sect. 4. FIBRILLOSAE Heim (1931). Pileus rarely subviscid, mostly dry; stipe never with marginate bulb, solid or hollow; context white to becoming pink in the stipe, sometimes bluing or greening in the pileus; odor very varied in the different species; excretive hyphae not very abundant; spores amygdaliform or elongate cylindric; muricate pleurocystidia always present; guaiac negative.

Type species: I. descissa (Fr.) Quél.

Stirps **Lucifuga** (Cortina persistent; stipe solid; lamellae initially with an olive tinge).

I. lucifuga (Fr. ex Fr.) Quel.; *I. deglubens* (Fr.) Gillet; *I. brunnea* Quel. apud Quél. & Le Breton; *I. eutheles* (Berk. & Br.) Sacc.; *I. posterula* (Britz.) Sacc. sensu Lange; *I. Pouzarii* Heim; *I. atripes* Atk.; *I. serotina* Atk.

Stirps **Descissa** (Cortina very fugacious; stipe hollow; lamellae not olive).

I. descissa (Fr.) Quel.

Stirps **Flocculosa** (Cortina silky; stipe solid; lamellae not olive).

I. flocculosa (Berk.) Sacc.; *I. tigrina* Heim.

Stirps **Lacera** (Lamellae initially flesh color ocher; stipe solid; spores cylindric).

I. lacera (Fr.) Quél.; *I. halophila* Heim; *I. pruinosa* Heim.

Stirps **Inconcinna** (Stipe solid; lamellae light olive then ferruginous; spores subamygdaliform; odor farinaceous).

Sect. 5. LILACEAE Heim (1931). Context lilac or violet in the stipe; spores not nodulose subangular; excretive hyphae rare; muricate pleurocystidia present; reaction with guaiac negative.

Type species : I. obscura (Pers. ex Fr.) Gillet.

Stirps **Obscura** (Cystidia without globulose « mucro »).

I. obscura (Pers. ex Fr.) Gillet; *I. cincinnata* (Fr.) Quel.

Stirps **Mucronata** (Cystidia with globulose « mucro »).

I. mucronata Heim.

Sect. 6. LACTIFERAE Heim (1931). Network of excretive hyphae very strongly developed; guaiac positive (purplish to blue) but reaction inconstant in *I. jurana* and negative in *I. praetervisa*; odor aromatic fruity, or of jasmine flowers or honey; context most frequently reddening on exposure.

Type species : I. piriodora (Pers. ex Fr.) Quel.

Stirps **Destricta** (Stipe vinaceous below).

I. jurana Pat.

Stirps **Piriodora** (Stipe not vinaceous below; carpophores not white; spores not nodulose subangular; muricate pleurocystidia present).

I. piriodora (Pers. ex Fr.) Quél.; *I. capucina* (Fr.) Karst.

Stirps **Subrubescens** (Lamellae distant; pleurocystidia none).

I. armoricana Heim; *I. subrubescens* Atk.

Stirps **Godeyi** (Carpophores entirely white and entirely reddening).

I. Godeyi Gillet; *I. Patouillardii* Bres.

Stirps **Bongardii** (Carpophores not entirely white; pleurocystidia none).

I. Bongardii (Weinm.) Quél. sensu Heim.

Stirps **Praetervisa** (Spores nodulose subangular).

I. grammata Quel. sensu Heim, non Kühner; *I. praetervisa* Quel. sensu Heim, non Kühner.

Sect. 7. SCABELLAE Heim (1931). Lamellae initially with a pinkish hue; excretive hyphae rare; short pleurocystidia muricate, constantly present; reaction with guaiac negative.

Type species : I. scabella (Fr.) Quel. sensu Cooke.

Stirps **Scabella** (Spores tuberculose-nodulose).

I. scabella (Fr.) Quél. sensu Cooke; *I. decipiens* Bres.; *I. globocystis* Vel.

Stirps **Splendens** (Lamellae chamois, then isabelline; odor slight).

I. splendens Heim; *I. Friesii* Heim.

Sect. 8. PETIGINOSAE Heim (1931). Pileus covered with a

tomentum, consisting of thick walled filaments; spores tuberculose-nodulose, small (6-7.5 µ); muricate pleurocystidia present.

Type species: I. petiginosa (Fr.) Gillet.

Stirps **Petiginosa** (Characters of the section).

I. petiginosa (Fr.) Gillet (Hebeloma, Quel.).

Sect. 9. GIBBOSPORAE Heim (1931). Pileus fibrillose squamose or woolly, sometimes rimose; stipe concolorous with the pileus; excretive hyphae rare; spores always tuberculate nodulose, or sometimes stellate with finger like spines.

Type species: I. maritima (Fr.) Karst.

Stirps **Maritima** (Lamellae thick and distant; spores with rounded angles or rectangular becoming grossly tuberculate nodulose).

I. maritima (Fr.) Karst.

Stirps **Boltonii** (Spores polygonal tuberculose-nodulose; stipe concolorous with the pileus).

I. Boltonii Heim; *I. Rennyi* (Berk. & Br.) Sacc.; *I. umbrina* Bres.; *I. margari[ti]spora* (Berk. apud Cooke) Sacc.; *I. Bucknallii* Mass.

Stirps **Lanuginosa** (Spores ovoid with numerous, i. e. 7-24, papillae; stipe concolorous with the pileus).

I. lanuginosa (Bull. ex Fr.) Quél. sensu Pat.

Stirps **Napipes** (Spores triangular, ovoid, tuberculose with few broadly conical papillae; stipe concolorous with the pileus, finely fibrillose-striate; pileus glabrescent, finally rimose fibrillose).

I. napipes Lange; *I. umboninota* Peck sensu Lange.

Stirps **Asterospora** (Stipe lighter colored than pileus).

I. asterospora Quél.

Stirps **Calospora** (Spores avoid globose with finger-like spines).

I. calospora Quél.

II

Compilation from Boursier and Kühner

Subgenus I. **Euinocybe** Lange (1917). Spores smooth, i. e. not nodulose subangular, or spiny.

(Not treated by Kühner)

Subgenus **Clypeus** (Britz.) Lange (1917). Spores nodulose suban-

present, inserted more or less high on the stipe which is therefore fibrillose, woolly or scaly; stipe generally brownish, at least in its lower portion and in age, often not bulbous and not marginate, with glabrous or pruinose apex but never pruinose in its entire length; context often inodorous or almost so; pleurocystidia rarely none, usually present, on the sides of the lamellae, and then often with thin or slightly thickened walls.

Type species *I. lanuginosa* (Bull. ex Fr.) Quel.

Stirps **Umbrina** [124] (Disc of the pileus not squarrose; spores with few, i. e. 12 or less, nodulose papillae).

I. pseudoasterospora Boursier & Kühner; *I. umbrina* Bres.; *I. napipes* Lange; *I. acuta* Boudier (I. umboninota Peck sensu Lange, Heim); *I. subcarpta* Boursier & Kuhne; *I. decipientoides* Peck [I. Astoriana Murr; I. ochraceoscabra Atk.; I. globocystis Vel.; I. carpta (Scop. ex Fr.) Sacc. sensu Ricken]; probably also *I. Bottoni* Heim.

Stirps **Lanuginosa** (Disc of the pileus squarrose; spores with more or less numerous papillae, i. e. up to 25).

I. Casimiri Vel.; *I. longicystidia* Atk.; *I. ovatocystis* Boursier & Kühner (These three species are meant to replace the indeterminable collective species *I. lanuginosa* (Bull. ex Fr.) Quél.).

Sect. 2. CALOSPORAE Kühner & Boursier (1932). Spores ovoid globose with spinose protuberances, at least 18; stipe entirely or almost entirely pruinose; marginate bulb at the base none.

I. calospora Quél.

Sect. 3. PETIGINOSAE Heim (1931). Cuticle of the pileus consisting of a hypodermium of inflated cells which are brownish, and an epicutis of hyaline filaments which are slender with thick walls; stipe entirely pruinose; base of the stipe not bulbous and not marginate; spores not as in the preceding section.

I. petiginosa (Fr.) Gillet [I. rufoalba Pat. & Doass.; I. scabella (Fr.) Quél. sensu Schröter].

Sect. 4. RUBELLAE Kühner & Boursier (1932). Context reddening when exposed to the air, bluing with guaiac; odor specific, or fruity, otherwise very close to the section *Marginatae* (sect. 5).

I. Bresadolae Mass. (I. grammata Quél. sensu Heim nec Quel. sec. Kühner & Boursier).

[124] Kühner uses the more general term « groupe » which is here interpreted

Sect. 5. **MARGINATAE** Kühner (1933). Cortina none, or inserted at the base of the stipe which consequently is entirely pruinose; stipe covered with dermatocystidia along its entire lenght, never fibrillose nor squamulose, usually white, pink, or yellowish, usually with a marginate bulb at the base; context not reddening on exposure; cystidia generally with thick walls.

Type species: *I. asterospora* Quél.

I. paludinella (Peck) Sacc.; *I. xanthomelas* Boursier & Kühner apud Kühner; *I. mixtilis* (Britz.) Sacc. sensu Kühner; *I. fibrosoides* Kühner; *I. praetervisa* Quél. sensu Kühner non Heim sec. Kühner [I. pseudomixtilis (Britz.) Sacc.]; *I. decipiens* Bres.; *I. grammata* Quél. sensu Kühner non Heim (I. albodisca Peck); *I. asterospora* Quél.; *I. pseudohiulca* Kühner; *I. oblectabilis* (Britz.) Sacc. sensu Kühner (I. hiulca var. major Bres.).

Note: Other presumably good species not included in Kühner's or Heim's work because they are known only from America or Asia, or from Europe, but undefined at the time of publication of these monographic papers, are all those indicated in *North American Flora*, *l. c.*, but not in the classifications indicated above, furthermore the following species from the Caucasus: *I. argentea* Sing.; *I. subaemula* (Britz.) Sacc. sensu Sing.; *I. devulgata* (Britz.) Sacc. sensu Sing., Kühner; *I. homomorpha* Sing.; *I. aemula* (Britz.) Sacc. sensu Sing.; *I. corrubescens* Sing. [I. relicina (Fr.) Quél. sensu Ricken]; *I. caucasica* Sing., and the following species from North America: *I. Kauffmanii* A. H. Smith (I. longipes Kauffman non Mass.); *I. olympiana* A. H. Smith; *I. multicoronata* A. H. Smith; *I. ferruginosa* A. H. Smith; *I. cystidiosa* (A. H. Smith) Sing. (Tricholoma cystidiosum A. H. Smith); *I. Hotsoniana* Stuntz; *I. calcata* Stuntz; from Europe: *I. pachycreas* Heim & Romagnesi; from South America: *I. variabillima* Speg. (= *I. decipientoides* Peck).

The following species described in other genera but actually belonging to *Inocybe* according to the type studies of the author, are: *I. praefarinacea* (Murr.) Sing. (Hebeloma, Murr.); *I. praevillosa* (Murr.) Sing. (Lepista, Murr.); *Inocybe pernicosa* (Murr.) Sing. (Entoloma Murr.); *I. mariluanensis* (Speg.) Sing. (Naucoria, Speg.); *I. Felipponei* (Speg.) Sing. (Collybia, Speg.).

KEY TO THE SPECIES

The author cannot present a key equal or superior to the existing keys. Those published in *North American Flora* by Kauffman (*l. c.*), by Heim (*l. c.*), and by Boursier & Kühner, Kühner & Boursier, and Kühner (in *Bull. Soc. Myc. Fr.*, l. c.) can be recommended. As far as the subgenus *Clypeus* is concerned, the keys published by Kühner and his collaborator have been tried out repeatedly by the author, and they were found to be very complete and reliable. As for illustrations, those published by Heim (*l. c.*) as well as those published in Lange's *Flora Agaricina Danica* should be consulted.

120. HEBELOMA (Fr.) Quél.

Champ. Jura Vosges, p. 128. 1872-73.

Type species: *H. fastibile* (Fr.) Quél.

Syn.: *Agaricus* trib. *Hebeloma* Fr., *Syst. Mycol.* **1**: 249. 1821.
Roumegueria Karst., *Bidr. Finl. Nat. Folk* **32**: xxiv. 1879.
Hylophila Quél., *Enchiridion* p. 98. 1886.
Myxocybe Fayod, *Ann. Sc. Nat.*, *Bot.* VII. **9**: 361. 1889.
Picromyces Batt. ex Earle, *Bull. N. Y. Bot. Gard.* **5**: 438. 1909.
Hebelomatis Earle, *l. c.*, p. 430.

Characters: Pileus viscid; epicutis consisting of strongly gelatinous and very thin filaments running mainly horizontally, hyaline, the terminal members not dermatocystidioid, i. e. not resembling the cheilocystidia; subcutis more irregular with melleous to rusty incrustations of pigment; lamellae pale argillaceous to pallid at first, later becoming deeper brownish but not bright or deep rusty in age (because of the sordid brownish color of the spore print [151]), often fimbriate or at least with a whitish edge (because of the large number of cheilocystidia); spores melleous, usually warty rough, usually fusoid to boat shaped, more rarely ellipsoid oblong or ellipsoid, frequently subacuminate at both ends, with a callus at the apex but without germ pore, without a plage, and sometimes practically smooth in bisporous forms; basidia tetrasporous, but bisporous forms not rare; pleurocystidia none; cheilocystidia hyaline, versiform, always distinct, crowded, making the edge of the lamellae heteromorphous; hymenophoral trama regular; stipe rather fleshy to fibrous fleshy, solid or hollow or stuffed, often pure white, and at least

[151] R. Maire indicates one species, *H. porphyrosporum* R. Maire, with porphyry brown spore print, not seen by the author. All our prints are « Clove » to « Coffee » (Maerz & Paul). Maire's species is said to be *H. sarcophyllum* (Peck) Sacc.

white at the apex of young specimens, never lilac or violet; the apex often squamulose or furfuraceous or pruinose, with cortina or without a distinct veil, sometimes with a distinct membranous veil which assumes the shape of an annulus in mature specimens of at least two species, at times the cortina also taking the shape of an annulus (*H. strophosum*); context inodorous, or more often with a characteristic odor, raphanaceous, of marzipan, chocolate, liqueur, hay, or tea leaves; pseudorrhiza sometimes present; context usually at least partly white; all hyphae with clamp connections. On the earth, on foliage, on fallen needles, rarely on decayed wood or in deep moss.

Development of the carpophores: Probably always hemiangiocarpous.

Area. Probably almost cosmopolitan.

Limits: Hebeloma is strictly intermediate between *Inocybe* and *Alnicola*. Some species have occasionally smooth spores, especially the bisporous forms, and these are then theoretically close to the Inocybes without metuloids. About the separation of smooth spored Hebelomas from these Inocybes, see under *Inocybe*. The smooth-spored Hebelomas may also come close to some species of *Pholiota*. *P. lenta* and *P. lubrica* are sometimes confused with *Hebeloma* but the chrysocystidia distinguish them immediately. *Pholiota albocrenulata* has once been transferred to *Hebeloma*, and here, the elongate spores and the absence of chrysocystidia seem to prove that this is a truly intermediate, transitional form. However, the general appearance, habitat, color of the spore print, and other less important characters link it with the rest of the *Pholiotae* more closely than with the Hebelomas, and it was therefore reunited with *Pholiota*.

There are several small *Naucoria*-like (collybioid) species of *Hebeloma* such as *H. pusillum* Lange and *Hebeloma Petrakii* (Hruby) Sing. which were studied thoroughly by the author. These small species might easily be confused with *Alnicola*, especially if anatomical characters such as the structure of the epicutis are neglected by the observer. If in these species the epicutis were made up of dermatocystidia or an epithelium, they would be inseparable from *Alnicola ciaculigera* and similar species of *Alnicola*. What has been described as *Alnicola dasypus* (Romagnesi), cannot be considered as an *Alnicola* since it has all the characters of *Hebeloma* including the epicutis as described by Romagnesi under the name of *Naucoria*

magnesi) Sing. There is no truly viscid species known in *Alnicola* thus far, and none has the epicutis made up of filamentous repent hyphae alone. *Alnicola clavuligera* Romagnesi is undoubtedly the one species of *Alnicola* that comes closest to *Hebeloma* because of the subviscid layer consisting of loosely arranged filamentous hyaline hyphae, exactly as in the pilei of the Hebelomas, yet these hyphae have terminal members which are non differentiated in *Hebeloma*, and dermatocystidioid in *Alnicola clavuligera*, i. e. they resemble the cheilocystidia. Romagnesi, on his part, doubts whether *Alnicola lignicola* Sing. is a true *Alnicola* without indicating the reasons why it should not be one. It is true that the spores are somewhat too deeply colored in NH_4OH as compared with the colors observed in other species of *Alnicola*. The spores and lamellae are, however, definitely not rusty enough for *Gymnopilus*, and it must be assumed that it does not belong in the latter genus as long as additional observations, especially of the spore print do not prove it to belong in this or some other genus.

Fortunately, the genus *Hebeloma* is characterized by a rather uniform external appearance. As soon as the beginner learns to distinguish genera in the agarics, he will remember the characteristic habit and colors of the Hebelomas, and he will soon, unerringly, identify the Hebelomas in the field, and aside from the few small species, there are rarely doubts as to whether a species belongs in *Hebeloma*. The pinkish cinnamon to ochraceous cinnamon color fading all the way to white near the margin (a few species are predominantly white), and tending to become deeper and richer reddish brown or fuscous in the center, combined with the dull brownish color of the lamellae and the whitish edges, the characteristic odor of many species, their viscidity and their habitat on the ground, give them away immediately.

State of knowledge : The intrageneric taxonomy of *Hebeloma* is completely confused. The few species which are more or less completely known have been interpreted differently by the authors. For example, Maire thinks that Ricken's *H. fastibile* is *H. crustuliniforme*, and his *H. crustuliniforme* is *H. fastibile*. There are a few more species which are reasonably well studied and named ; the remaining species are in a complete chaos. The classification of the species is unsatisfactory. The author refrains from adopting any of the possible classifications, and merely lists thirteen species in alphabetical

Practical importance : It seems to be quite certain that at least one species of *Hebeloma* is poisonous Some confusion in the statements on this subject can easily be explained by the fact that those reporting the edibility, or non-edibility of Hebelomas, did not always have the same species in mind when using the same specific epithet. The question of *Hebeloma* poisoning cannot be solved satisfactorily unless the taxonomy of *Hebeloma* is revised previously.

SPECIES

H. anthracophilum R. Maire ; *H. austroamericanum* (Speg.) Sacc. ; *H. crustuliniforme* (Bull. ex Fr.) Quél. ; *H. dasypus* (Romagnesi) Sing. (Naucoria, Romagnesi ; Alnicola, Romagnesi); *H. fastibile* (Fr.) Quél.; *H. mesophaeum* (Pers. ex Fr.) Quel. ; *H. pascuense* Peck ; *H. Petrakii* (Hruby) Sing. (Naucoria, Hruby) ; *H. pusillum* Lange ; *H. radicosum* (Bull. ex Fr.) Ricken (Pholiota. Quél. ; Myxocybe, Fayod ex aut.) ; *H. sacchariolens* Quél. ; *H. sinuosum* (Fr.) Quél. sensu R. Maire [H. claviceps (Fr.) Gillet sensu Ricken] ; *H. strophosum* (Fr.) Sacc. sensu Ricken (Roumegnerites, Karst.).

KEY TO THE SPECIES

It is evident that under the circumstances indicated in the paragraph on the « state of knowledge », it is impossible to provide a key for the determination of the species.

121. **ALNICOLA** Kühner

Contrib. à l'Etude des Hymenomycètes, p. 175 Paris 1926

Type species : *A. submelinoides* Kühner.

Characters : Pileus subviscid to dry, squamulose, fibrillose, or glabrous, epicutis consisting of dermatocystidia, or at least containing numerous dermatocystidia which appear as the terminal members of the cuticular hyphae, or else consisting of spherocysts which often form a true epithelium ; spores warty or punctate without suprahilar smooth disc (plage), in shape and color agreeing with those of *Hebeloma*, argillaceous brown to umber sepia, or a very dull ferruginous brown in print, usually rather large (i. e. more than 9 µ

lae heteromorphous, always numerous and conspicuous but sometimes very narrow; hymenophoral trama hyaline or colored, almost subregular to regular; basidia often bisporous, otherwise normal in all regards; pleurocystidia none, or very few and then not different from the cheilocystidia and not far apart from the very edge of the lamellae; stipe central, often elongate, longer than the diameter of the pileus, thin, usually colored, more or less cortinate but cortina sometimes quite indistinct; context fleshy but thin, consisting of hyphae with or more rarely without clamp connections. On the ground, on foliage, rarely on wood, or on charcoal, frequently under *Alnus* or *Salix*.

Development of the carpophores : Probably always hemiangiocarpous.

Area : Northern-temperate and boreal, more frequent and also richer in species in Europe and Asia than in America, at least in the Eastern United States; at least three species occur in extratropical South America.

Limits : Alnicola is precisely intermediate between *Hebeloma* and *Naucoria*. Its delimitation is discussed in the latter two genera.

State of knowledge : The fourteen species entering this genus are all well known thanks to special papers devoted to the taxonomy and cytology of *Alnicola* by Kühner and Romagnesi. The development of the carpophores has not been studied in detail as far as is known to the author, but a superficial observation of « buttons » seems to indicate that the development of the carpophores is not or not much different from that of *Hebeloma*.

Practical importance : No economic importance is at present credited to the Alnicolas but their alnophilous habitat is often caused by a mycorrhizal relationship between these fungi and *Alnus* spp.

SPECIES

Sect. 1. **SUBMELINOIDEAE** Sing. (1939). Cheilocystidia usually rather thick, not attenuate or acute at the apex.

Type species : A. submelinoides Kühner.

A. clavuligera Romagnesi; *A. bohemica* (Vel.) Sing. (Naucoria, Vel.); *A. submelinoides* Kühner; *A. alnetorum* (R. Maire apud Kühner) Romagnesi; probably also *A. lignicola* Sing., and obviously *A. pseu-

doamarescens Kühner & Romagnesi, also one undescribed species from Argentina.

Sect. 2. **MELINOIDEAE** Sing. (1930). Cheilocystidia narrow, tapering to a subacute or acute apex or broadly rounded and tapering cheilocystidia mixed, the latter predominating in adult caps.

Type species: A. melionoides (Fr. sensu Ricken) Kühner.

A. amarescens (Quél.) Romagnesi (Naucoria, Quél.); *A. luteolofibrillosa* Kühner; *A. suavis* (Bres.) Kühner (Naucoria, Bres.); *A. umbrina* (R. Maire) Sing. (Tubaria, R. Maire; Naucoria, R. Maire non Bres.; Alnicola badia Kühner nom. subnud. 1926 ex Kühner 1931; Naucoria phaea Kühner & R. Maire apud R. Maire; Naucoria, spec. Sing. 1929); *A. melinoides* (Fr. sensu Ricken, Sing.) Kühner [Naucoria, Quél.; Naucoria escharoides (Fr.) Quél. sensu Konr. & Maubl. vix (Fr. non Secr.); Alnicola, Romagnesi]; *A. scolecina* (Fr. sensu Lange) Romagnesi; — also one undescribed species from Argentina.

KEY TO THE SPECIES

The key below is the key published by Romagnesi, with a few changes introduced by the author.

A. Cheilocystidia broad, rounded above.

B. On the ground or on foliage, sometimes in deep moss

C. Cuticle consisting of loosely arranged hyphae with the terminal members dermatocystidioid, resembling the cheilocystidia, capitate; pileus subviscid. France. *A. clavuligera*

C. Cuticle with a different structure; pileus completely dry

D. Clamp connections present. Europe.

E. Basidia 4-spored. *A. submelinoides*

E. Basidia 2-spored. *A. alnetorum* [126]

D. Clamp connections absent. Europe, Northern Asia, and North America. *A. bohemica*

B. On decaying wood of *Picea Schrenckiana*, Central Asia (see *A.* (?) *lignicola*)

B. On burned ground. France. (see *A. pseudoamarescens*)

A. Cheilocystidia narrow, tapering upwards and acute or subacute at the apex.

F. On charcoal; taste bitter. Europe *A. amarescens*

F. Either not on charcoal or not bitter.

G. Pileus pallid to light ocher under a fibrillose coating. Europe and North Asia. *A. luteolofibrillosa*

G. Pileus more strongly pigmented, or glabrescent

[126] In Romagnesi's key, *A. alnetorum* is indicated as 4-spored, and *A. submeli-*

H. Odor aromatic-fruity; spores scarcely longer than 10 μ. Europe and North Asia. *A. suavis*

H. Odor none, or very weak and not aromatic-fruity; spores usually reaching more than 10 μ in length.

I. Taste mild. Europe, Caucasus, and North Africa. *A. umbrina*

I. Taste more or less bitter.

J. Pileus silky-fibrillose. Europe, North Asia, North America. *A. melinoides*

J. Pileus subvelutinous when young, glabrescent and slightly granulose when adult. Europe, and also in America. *A. scolecina*

122. NAUCORIA (Fr.) Quél.

Champ. Jura Vosges, p. 131. 1872-73, em.

Type species : Agaricus (Naucoria) centunculus Fr.

Syn. : *Agaricus* trib. *Naucoria* Fr. *Syst. Mycol.* 1 : 60. 1821.
Simocybe Karst., *Bidr. Finl. Natur Folk* 32 : xxii. 1879.

Characters : Small mycenoid or collybioid carpophores, rather fragile and thin, often growing on wood and other plant debris; pileus hygrophanous, hemispheric to repand with slightly incurved margin or with straight margin when young; epicutis consisting of erect hyphae with numerous dermatocystidia forming the thermonal members of the trichodermium-palisade or trichodermium; lamellae adnate to adnexed subfree; spore print about Pl. 15, J-12 (Maerz & Paul) (in *N. alachuana*) and between « Seminole » and « Wigwam » (Maerz & Paul) (in *N. tiliophila* and other species), generally not much different from that of *Hebeloma* and *Alnicola*; spores under microscope melleous, smooth, without germ pore but often with a distinct callus, reniform phaseoliform to ellipsoid or ellipsoid to ellipsoid oblong or almost boatshaped but usually with attenuate but obtuse or with rounded ends, with moderately thick, indistinctly to distinctly double (endosporium and episporium) wall, small to rather large; basidia quite normal but sometimes 2 spored; cheilocystidia always present, usually making the edge of the lamellae distinctly heteromorphous; pleurocystidia none; hymenophoral trama regular; hyphae usually with clamp connections; stipe thin, with a very slight and fugacious veil or practically naked even when young; pseudorhiza not present in the species known.

Development of the carpophores : Probably hemiangiocarpous.

Area : Almost cosmopolitan.

Limits: This genus differs from the preceding genera in having smooth spores. This character which, in the tribus *Inocybeae,* it has in common only with *Inocybe,* makes it possible to distinguish the *Naucoriae* from the *Alnicolae.* Otherwise, this latter genus is very closely related to *Naucoria.* Since the line between the species of each of these genera is a sharp one, and seems to be correlated with a certain difference in the biological relationship between the accompanying flora and the fungi of these genera — a relationship absent, or at least not ovious and certainly not limited to *Alnus* and *Salix* in *Naucoria* — the author believes that *Alnicola* is generically separable from *Naucoria*, a belief that has become a conviction since the type studies made during the last few years on subtropical and tropical material corroborated all the data obtained on temperate species. In fact, *Alnicola* seems to be absent in the subtropics and tropics, at least in America, and it is now possible to add a third correlated character to the two mentioned previously : the geographic distribution.

Naucoria differs from *Inocybe* by a number of characters, mainly the structure of the epicutis. In *Inocybe*, the epicutis does not consist of a trichodermium palisade whose terminal members are dermatocystidioid, and no spherocysts are present.

The author did not distinguish generically between *Naucoria* and *Phaeomarasmius* as far as species without distinctly pilose covering were concerned. This led to a situation where the limits between *Phaeomarasmius* and *Naucoria* became rather indistinct, and several species of *Phaeomarasmius* were left within *Naucoria* where they had been placed by Fries. Romagnesi emphasized the hygrophanous pileus in *Naucoria* and the mostly non-hygrophanous pileus in *Phaeomarasmius.* The author accepts this point of view as the best delimitation between the two genera available at present. However, it must be admitted that it will be necessary to find correlated characters in order to prove this somewhat arbitrary line of demarcation actually to be a hiatus between two good genera. While accepting Romagnesi's view, the author expresses the conviction that this will be more readily acceptable as soon as more and better observations on the color of the spore print will be available, all checked in perfectly fresh condition with the equivalent in Maerz & Paul, or Ridgway, or Seguy.

the species of *Naucoria* have been pointed out in the preceding paragraph. A purely macroscopical description, often not accurate for the fresh carpophores, has little significance for the determination of a species of this genus. This makes it understandable that a large number of careful type studies on Naucorias is still required in order to separate all the foreign elements — such as other genera of the *Cortinariaceae*, Agrocybes, Pholiotinas — from the true Naucorias. Only this procedure will make it possible to compile all the material necessary for a monograph. Among the species enumerated below, only those have been admitted which are perfectly well known in the essential characters (though not always concerning the exact color of the spore print and never concerning the individual development of the carpophores), and are not identical with each other. It must be emphasized, however, that these species are by far not the only ones in existence. On the contrary, the number of species of *Naucoriae* and *Phaeomarasmii* in the southern portion of North America is rather large and largely unexplored (except for a few species described by Murrill from North Florida), and even in the northern part of the continent, the Naucorias have found little interest among the mycologists. Consequently, it may be expected that the number of species, which is now seven, will grow steadily as farther type and field studies progress.

Practical importance : None.

SPECIES

N. tiliophila (Peck) Sing. (Crepidotus, Sacc.); ***N. centunculus*** (Fr.) Quél.; ***N. reducta*** (Fr.) Sacc. sensu Lange, Romagnesi; ***N. effugiens*** Quél.; ***N. atomacea*** (Murr.) Sing. (Atylospora, Murr.); ***N. alachuana*** Murr. (Psilocybe alachuana, Murr.); ***N. melleiceps*** (Murr.) Sing. (Galerula, Murr.).

KEY TO THE SPECIES

Since the list of species above contains only a fraction of the species in existence the author refrains from adding a key and refers to the original and emended descriptions of these species.

Tribus CORTINARIEAE Fayod

Prodrome, Ann. Sc. Nat., Bot. VII **9**: 371, 1889 ut tribus *Agaricearum*, *Cortinaries*,; Kühn. & Maubl., *Icon. Sel. Fung.* **6**: 122, 1924-37 (item); Imai, *Journ. Fac. Agriculture Hokk. Imp. Univ.* **43** (2): 200, 1938.

Type genus : Cortinarius Fr.

Syn. : Cortinariaceae subfam. *Cortinarioideae* Sing., *Ann. Myco.* **34**: 341, 1936, p. p.
Cortinariaceae subfam. *Galerinoideae* Sing., *Ann. Mycol.* **34**: 342, 1936, p. p.

Characters : Those of the family, but with rusty brown to bright ferruginous fulvous spore print; spores never nodose subangular and never stellate spinose; plage often present; cheilocystidia either present or absent.

KEY TO THE GENERA

A. Veil distinctly membranous and distinctly double consisting of an apical annulus and an annular volva beneath when mature, both whitish; cystidia none; spores broadly amygdaliform, verrucose, without plage, bright rusty in print. 123. *Rozites*

A. If the veil is double, at least the inner veil is a cortina; the outer veil may then be membranous, glutinous, or also a cortina; if the veil is simple, it is either membranous or it is a cortina; cystidia present or absent; spores as described above, or different.

B. Spores roughened to warty, echinate-spinose, or with irregular thin ornamentation forming areolae, with or without a plage.

C. Spores without a plage.

D. Clamp connections absent (see *Galerina*, sect. *Tubarioides*).

D. Clamp connections present.

E. Stipe central, large, either very thick, and voluminous, or in an average longer than the diameter of the pileus, usually straight or somewhat flexuous, growing on wood or on other substratum.

F. Cortina present.

G. Mycelium growing in the forest soil, usually forming mycorrhiza with forest trees; cheilocystidia and pleurocystidia sometimes present, but more often absent, especially in those forms that turn black with alkali or grow on wood (very few do). 124. *Cortinarius*

G. Mycelium usually growing on wood (sticks, cortex, stumps, logs, trunks, etc.), on grass roots, etc., rarely on orchids with which it might form endotrophic mycorrhiza; cheilocystidia always present;

cheilocystidia ; pileus in most species blackening with KOH, especially when covered with spore dust. 126. *Gymnopilus*

F. Cortina absent ; veil strictly membranous, or none.

H. Veil present or absent ; pileus viscid (then with veil), or dry ; external appearance like *Pholiota* (see *Gymnopilus*)

H. Veil absent ; pileus viscid or lubricous ; external appearance collybioid ; stipe often a pseudorhiza.

I. Spore print ochraceous. 125 *a*. *Descolea*

I. Spore print bright rusty. 127. *Phaeocollybia*

E. Stipe very small, strongly curved, very short and rather thin, eccentric to lateral or almost absent 128. *Pyrrhoglossum*

C. Spores with a plage (smooth suprahilar disc) 129. *Galerina*

B. Spores completely smooth.

K. Stipe not bulbous and marginate 130. *Phaeomarasmius* [1]

K. Stipe thick, fleshy, bulbous, marginate 123. *Leucocortinarius*

123. ROZITES Karst.

Hattsr. ; Bidr. Finl. Nat. Folk 32 : xx. 1879.

Type species : R. caperata (Pers. ex Fr.) Karst.

Characters : Pileus with an epicutis consisting of a rather thick layer of parallel, repent, smooth, filamentous hyphae, without any dermatocystidia ; lamellae pale rusty colored, adnate ; spore print light but bright rusty colored near « Argus brown » (Ridgway) or « Sudan brown » (Maerz & Paul) ; spores under the microscope melleous with rusty brown warts, broadly amygdaliform, rather voluminous, without plage, without germ pore ; basidia normal, tetrasporous ; cystidia none ; cheilocystidia scattered, inconspicuous and inconstant and not making the edge of the lamellae heteromorphous ; hymenophoral trama regular ; stipe without pigment (pigment virtually restricted to the cuticle and the spores, and not abundant), with double veil, consisting of an upper membranous veil which forms an apical annulus in mature specimens, and a less distinct outer veil which usually forms a volval belt or an annuliform volva in the lower part of the stipe, both veils whitish and membranous. Carpophores rather large and fleshy, growing directly on forest soil ; all hyphae with clamp connections ; hymenophore develops HCN.

Development of the carpophores : Hemiangiocarpous ; the lamellae

[1] If the epicutis consists exclusively of repent hyphal elements, see *Gale...*

are probably formed by folding of the partial veil (according to Kühner); data supporting the hemiangiocarpous development of *R. caperata* were first published by Sawyer (1917).

Area: Temperate regions, with certainty known only from the northern hemisphere.

Limits: This genus differs from the other *Cortinariaceae* in the whitish, membranous, double veil. The broad amygdaliform spores with their strong warts and lacking plage and the strictly filamentous cutis of the pileus which is neither viscid nor scaly, nor hygrophanous, offer additional characters valuable for the separation of this good and natural genus.

The emendation proposed by Singer (1923) whereby *Pholiota spectabilis* would have been included in *Rozites* because of its rough spores, has since then been made impossible by the definition of the genus *Fulvidula* = *Gymnopilus*. The simple veil and the crowded cheilocystidia, smaller spores and more richly colored spores print, more abundant pigmentation and lignicolous habitat distinguish *Gymnopilus spectabilis* (*Pholiota*, *Fulvidula*, etc.) from *Rozites*.

State of knowledge: Only one species is known with certainty. Overholts seemed to think that *Pholiota McMurphii* Murr. belongs in the close neighborhood of *Rozites caperata* as he says that « this species is close to if not identical with *P. caperata* ». The shiny pileus and the different veil make it impossible to insert this species in *Rozites* as the latter is defined at present, and if it should actually turn out to be congeneric with *R. caperata*, the characters must be rechecked, and if the glutinosity of the pileus and the singleness of the veil should be proved to be constant characters of *P. McMurphii*, the generic diagnosis of *Rozites* must be emended. It appears rather improbable that this should be the case, yet, in monotypic genera, it is always wise to admit the possibility of later emendations rather than to apply the original diagnosis in too strict a manner.

Practical importance: If *Rozites* belongs among the mycorrhizal fungi which has been suggested by some observers, it is not a specialized one, for *R. caperata* is not selective in regard to its habitat; it is equally frequent in coniferous as in frondose woods. But it may have some future importance in forestry. This species is also known as a good edible mushroom widely known in some regions of Europe under the name « gypsy » (or corresponding names in other languages). The species said to be « cultivated » by ants in South America, is not a *Rozites* (see under *Agaricus*).

SPECIES

R. caperata (Pers. ex Fr.) Karst. (Pholiota, Gillet; Cortinarius, Fr.).

124. CORTINARIUS Fr.

Genera Hymenomycetum, p. 7. 1836.

Type species : *C. violaceus* (L. ex Fr.) Fr.

Syn : *Cortinaria* (Pers. ex Fr.) S. F. Gray, *Nat. Arr. Brit. Pl.* **1** : 627. 1821 (proposed for rejection)
Dermocybe (Fr.) Fayod, *Ann. Sc. Nat. Bot.* VII. **9** : 372. 1899.
Hydrocybe (Fr.) Fayod, *l. c.* p. 372.
Telamonia (Fr.) Fayod, *l. c.* p. 373.
Myxacium (Fr.) Fayod, *l. c.* p. 374.
Phlegmacium (Fr.) Fayod, *l. c.* p. 375.
Agaricus tribus *Telamonia* Fr., *Syst. Mycol.* **1** : 210. 1821.
Agaricus tribus *Phlegmacium* Fr., *l. c.* p. 226.
Agaricus tribus *Dermocybe* Fr., *l. c.* p. 227.
Agaricus tribus *Myxacium* Fr. *l. c.* p. 247.
Cortinarius subgen. *Hydrocybe* Fr., *Epicrisis* p. 303. 1838.
Sphaerotrachys Fayod, *l. c.* p. 374
Gomphos Kuntze, *Rev. Gen. Pl.* **2** : 835. 1891.
Inoloma (Fr.) Earle, *Bull. N. Y. Bot. Gard.* **5** : 441. 1909 [144]
Agaricus tribus *Inoloma* Fr. *Syst. Mycol.* **1** : 216. 1821 [145].
Bulbopodium Earle, *l. c.* p. 441.
Hydrocybium Earle, *l. c.* p. 440.
Meliderma Vel. *České Houby*, p. 399 : 1920.
? *Cystocybe* Vel., *l. c.* p. 495, ad int. (not validly published)

Characters : Habit very variable, from mycenoid to collybioid, clitocyboid, tricholomatoid to nearly pluteoid; pileus glutinous, viscid, or hygrophanous, or dry and neither viscid nor hygrophanous, and then squamose, squamulose, rimose, fibrillose, sericeous, or glabrous, sometimes even tomentose or innately floccose; lamellae subfree to decurrent, narrow to broad, with various colors in young specimens (according to species and sections), later usually becoming very deeply and richly colored, charasteristic even in mature well dried

[144] Earle (*l. c.*) and Kauffman in *North American Flora* **10** : 282. 1932 cite Karsten, *Medd. Soc. Fauna Flora Fenn.* **18** : 70. 1891 as the first to marke the tribus *Inoloma* a genus. However, Karsten merely cites one species as occurring in Finland which he names « *Inoloma opimum* Fr. ». This is not a valid publication of a new status.

material, deep rusty and somewhat dusty in most cases from the spore print of the same color; spores rusty ocher to melleous under the microscope, usually deep colored in ammonia mounts, more or less distinctly warty-rough, but never actually smooth, without suprahilar plage and without a germ pore but often with a distinct callus; consisting of at least an episporium and an endosporium, the ornamentation perhaps of exosporial origin, a perisporium also often evident, globose, subglobose, ellipsoid, ellipsoid-oblong, cylindric-oblong, amygdaliform, etc.; basidia 4-spored, very rarely 2-spored; cystidia rarely present on the sides of the lamellae, more often on the edges (cheilocystidia); hymenophoral trama regular; stipe central, with a cortina which may be attached to the base or to the apex of the stipe (with all intergradations and with varying width of the zone of attachment), connecting with superficial fibrils of the pileus, later often characteristically dusty with the rusty spores; frequently there is a second, outer veil present which forms a low annulus (annulus inferus) which is usually attached to the stipe, and is then called belt; sometimes, especially in *Telamonia*, there are several such belts which may be white, bright colored, or brown to concolorous; a purple to vinaceous, or bluish to violet color is often present on the stipe, and on the young lamellae, sometimes also on the pileus; the stipe may be covered by a glutinous outer veil *(Myxacium)* and then the pileus is also glutinous; context consisting of hyphae with clamp connections; the brownish, reddish and yellow pigments usually incrusting the walls of the hyphae; odors often characteristic; taste mild or bitter. On earth and humus in woods and near trees.

Development of the carpophores: Hemiangiocarpous, according to the data of Douglas, Sawyer, and Kühner.

Area: The species of *Cortinarius* are common in the boreal and mountain regions of the northern hemisphere and become gradually somewhat less abundant in the warmer belt of the temperate zone but reach another high as far as the number of species and individual carphores is concerned in the winter rainy season in North Florida and adjacent regions of North America. North America, Europe and Asia are about equally rich in species. *Cortinarius* also occurs in South America (Southern Brazil, Argentina and South Chile), parts of Africa and Australia. In the tropics, the genus is represented by very few species and individuals.

Limits: The genus *Cortinarius* is not easy to define because of the

yet there are few genera in the *Agaricales* that can be recognized in the field as easily as *Cortinarius*, even by the beginner.

Cortinarius « touches » certain closely related genera such as *Gymnopilus* (closest to the subgenus *Dermocybe*), *Galerina* (closest to subgenus *Hydrocybe* and *Telamonia*), and *Rozites* (closest to *Inoloma*). However there should not be any real difficulty in distinguishing these genera from *Cortinarius* if the key is used wisely. Only one species of *Cortinarius* is reported as growing on wood (many species may grow on very decayed wood coincidentally rather than habitually), viz. *C. lateritius* (Pat.) Sing. (Flammula, Pat.). This is the only instance where a *Cortinarius* had been misdetermined as a *Flammula* of the *Sapineae* group, i. e. *Gymnopilus*. The opposite has happened with *Gymnopylus intermedius* (Sing.) Sing. which was once tranferred to *Cortinarius* and with *C. punctifolius* Peck which is a *Gymnopilus*. But both these species are not atypical for their respective genera, and their position is now beyond doubt.

State of knowledge : Some species of *Cortinarius* have been completely studied by Henry and A. H. Smith. These authors are now beginning to publish keys for certain groups, especially in *Phlegmacium*. In spite of some excellent work done by several authors in the past, the majority of the species is still insufficiently defined or the interpretations are at variance. Henry's papers suggest that many of the older species are collective though they may not have been collective in Fries' personal concept. As for the macroscopical characters, Fries' *Monographia* is still one of the most important sources for North European species. Ricken and Velenovsky gave excellent accounts with indications of spore characters, and — where observed — cystidia. In addition, microscopical characters were indicated by Kauffman (in *North American Flora*, *l. c.*) and by A. H. Smith in various papers, illustrated with excellent photographs. Chemical characters appear to be of great assistance in the identification and classification of the *Cortinarii* as is shown by Henry's papers. Unfortunately the latter author is thus far the only one to use them. A careful study of the various types of pigments as well as a more detailed study of the cortical layers of both pileus and stipe, and other anatomical characters, including the size and shape of the cheilocystidia in such groups as *Hydrocybe* would also materially help to solve some of the difficulties encountered in the study of the *Cortinarii*. A group as vast and difficult as this should not be approached without exhausting all characters available, including

mycorrhizal specialization, pigment topography and perhaps studies on the sexuality.

Since the state of knowledge of *Cortinarius* does not allow to draw a definite conclusion at the time this is written, it seems to be wiser to wait for a monographic treatment rather than to attempt to present an interim classification with an enumeration of certain species which would necessarily be arbitrarily chosen, and of little help to those who desire a certain amount of information about the status of our present knowledge on the *Cortinarii*. Since this information can easily be obtained by a study of the literature (Fries, Ricken, Henry in *Bulletin de la Société Mycologique de France* and *Revue de Mycologie*; Kauffman in *North American Flora* and in the *Agaricaceae of Michigan)*, there is, in the author's opinion no urgent need for a detailed treatment of the genus in the present work. The number of species admitted here is inconsequential since it reflects only the sum of examples rather than an enumeration of the species. The real number of *Cortinarii* is probably several hundred.

This policy of giving examples rather than enumerations appears to be necessary inasmuch as none of the authors working on the genus has thus far proposed any important change in the traditional classification of the species within *Cortinarius*; yet, such changes and rearrangements appear to be inavoidable in the future in spite of the fact that the classification of Fries and also that of Kauffman are less unsatisfactory than other intrageneric classifications proposed at that time. It seems that *Inoloma* and *Dermocybe* are not well separated in the present scheme, and *Telamonia* and *Hydrocybe* may not be separable as subgenera on the same level as *Myxacium* and *Phlegmacium*.

Nevertheless, the Friesian scheme is reproduced here, considering that only careful investigations of specialists will in the end produce a new more satisfactory classification. The Friesian scheme has been accepted temporarily without prejudice against Kauffman's admission of *Bulbopodium*, or Fayod's admission of *Sphaerotrachys*, both of which may eventually turn out to be useful units in a revised system of classification of the *Cortinarii*.

The author does, however, take a stand in regard of the delimitation of the genus *Cortinarius*. The trend toward smaller genera that, to a certain degree, characterized some phases of the modern ap-

very large genera such as *Cortinarius. Cortinarius* is by no means more heterogeneous than any other genus in the *Cortinariaceae,* and its restriction to *Telamonia* as proposed by Earle, or its abandonment in favor of six or seven autonomous « genera » (which is aside from being taxonomically wrong, also illegal according to the International Rules of Nomenclature), should not be advocated any more than the dismemberment of the genus *Russula* (also proposed by Earle), or any other large homogeneous genera.

Practical importance : The *Cortinarii* will probably become important in forestry when the fungus flora in the temperate zones is looked upon as a potential factor in the rate and quality of development of the trees under certain ecologic conditions. Most of the *Cortinarii* appear to be mycorrhizal fungi, and some are considerably specialized in their associations with *Cormophyta.* Some species are known to be edible but few are used in large quantities.

SPECIES

Subgenus **Myxacium** (Fr. 1821) Fr. (1836-38). Pileus and stipe viscid, or pileus viscid and stipe not bulbous and taste bitter.

Type species : C. collinitus (Pers. ex Fr.) Fr.

Stirps **Collinitus** (Stipe with floccons covered by the mucus).

C. collinitus (Pers. ex Fr.) Fr. ; *C. elatior* Fr. ; *C. alpinus* Boud., etc.

Stirps **Delibutus** (Stipe merely viscid).

C. delibutus Fr. ; *C. luteoalbus* (Sing.) Sing. ; *C. causticus* Fr., etc.

Subgenus **Phlegmacium** (Fr. 1821) Fr. (1836-38). Pileus viscid ; stipe dry ; taste mild.

Type species : C. decoloratus (Fr.) Fr.

Sect. CLIDUCHI Fr. (1836-38). Stipe thickened below but not marginate-turbinate.

Type species : C. cliduchus Fr.

C. vitellinopes (Secr.) Sing. (Agaricus, Secr. ; C. cliduchus Fr.) ; *C. varius* (Schaeff. ex Fr.) Fr. ; *C. infractus* (Pers. ex Fr.) Fr., etc.

Sect. SCAURI Fr. (1836-38). Stipe at the base marginate bulbous ; the cortina is attached to the marginate portion of the bulb.

Type species : C. caerulescens (Schaeff. ex) Fr.

C. caerulescens (Schaeff. ex) Fr. ; *C. glaucopus* (Schaeff. ex Fr.) Fr. ; *C. calochrous* (Pers. ex Fr.) Fr. ; *C.* [illegible] A. H. Smith, etc.

Sect. **ELASTICI** Fr. (1836-38). Stipe without a bulb, often stuffed or flexuous when old; cortina often scanty and fugacious.

Type species: C. olivascens (Batsch ex) Fr.

C. olivascens (Batsch ex) Fr.; *C. decoloratus* (Fr.) Fr., etc.

Subgenus **Inoloma** (Fr. 1821) Fr. (1836-38). Pileus and stipe dry; pileus initially silky because of innate fibrils or scales; stipe fleshy, subbulbous in many species.

Type species: C. violaceus (L. ex Fr.) Fr.

Ricken divides this subgenus in two — as it seems, rather natural — groups:

a) Spores amygdaliform [the type species of the subgenus and *C. hircinus* Fr.; *C. alboviolaceus* (Pers. ex Fr.) Fr.; *C. traganus* (Fr.) Fr., etc.].

b) Spores globulose [*C. callisteus* Fr.; *C. bolaris* (Pers. ex Fr.) Fr.].

Note: Group (*b*) is very close to *Dermocybe* and perhaps not separable from it.

Subgenus **Dermocybe** (1821) Fr. (1836-38). Pileus non-viscid and non hygrophanous, silky to subvelutinous, glabrescent, rather thin; stipe equal or attenuate toward the base, stuffed or hollow, the cortical layer rigid.

Type species: C. cinnamomeus (L. ex Fr.) Fr.

The central group, very natural and characteristic, is the group with bright colored lamellae, the subtribus *Raphanoideae* Fr. 1821, p. p. The following species may serve as examples: *C. cinnamomeus* (L. ex Fr.) Fr.; *C. semisanguineus* (Fr.) Gillet; *C. cinnabarinus* Fr.

Other species are: *C. anomalus* (Fr. ex Fr.) Fr.; *C. caninus* (Fr.) Fr.

Subgenus **Telamonia** (Fr. 1821) Fr. (1836-38). Pileus hygrophanous and not viscid; external (outer) veil present, forming a belt or belts below the cortina.

Type species: C. torvus (Fr.) Fr.

C. haematochelis (Bull. ex) Fr.; *C. armillatus* (Fr.) Fr.; *C. gentilis* (Fr.) Fr.; *C. helvelloides* (Fr.) Fr.; *C. flavornatus* Sing.; *C. hinnuleus* (Sow. ex Fr.) Fr.; *C. helvolus* (Bull. ex) Fr.; *C. punctatus* (Pers. ex) Fr. sensu Lange; *C. bivelus* (Fr. ex Fr. p. p.) Fr.; *C. torvus* (Fr.) Fr.; *C. evernius* (Fr. ex Fr.) Fr.; *C. scutulatus* (Fr.) Fr.; *C. rigidus* (Scop. ex) Fr. sensu Ricken; *C. hemitrichus* (Pers. ex Fr.) Fr.; *C. heterosporus* Bres.

Subgenus **Hydrocybe** Fr. (1836-38). Characters as in *Telamonia* but veil consisting of the cortina exclusively.

C. renidens Fr.; *C. balaustinus* Fr.; *C. saturninus* (Fr.) Fr., *C. tortuosus* (Fr.) Fr.; *C. erythrinus* (Fr. ex Fr.) Fr.; *C. uraceus* Fr.; *C. holophaeus* Lange; *C. saturatus* Lange; *C. sciophyllus* Fr.; *C. suniosus* (Fr.) Fr.; *C. decipiens* (Pers. ex Fr.) Fr.; *C. obtusus* (Fr.) Fr.; *C. Junghuhnii* Fr.; *C. acutus* (Pers. ex Fr.) Fr.; *C. insignis* Britz.; *C. nigricans* (Vel.) Sing. (Hydrocybe, Vel.), etc.

KEY TO THE SPECIES

The species of the North America Continent are keyed out in Kauffman's work, cited twice before (*North America Flora*, **10** (5): 282-290. 1932); but many species described later must be looked up in the original papers by A. H. Smith and W. A. Murrill [159].

The species of Europe can be determined by using Lange's keys, with consultation of such works as Ricken's *Blätterpilze* and Bresadola's *Iconographia Mycologica*. Lange's keys, descriptions and colored figures were republished in Lange, *Flora Agaricina Danica*, **3**: 7. 1938.

More complete keys have been published for certain groups of *Cortinarius*. The American species of *Bulbopodium*, i. e. *Phlegmacium* sect. *Scauri*, can be determined satisfactorily with the key published by A. H. Smith in the *Bull. Torr. Bot. Cl.* **69** (1): 43-48. 1942. The European species of the same group are treated in a key published by Henry in *Revue de Mycologie, Supplément* **8** (2): 1-56. 1943. He indicates many American species in his key, and it is not quite clear whether he has studied them himself, and whether he thinks that they occur in Europe. Another key containing the sections *Cliduchi* and *Elastici* was published in the same journal by the same author [*Rev. Myc.* **10**: 44-82 (supplément). 1945 (published 1946)].

The Australian species can be determined with the keys and descriptions given by Cleland, *Toadstools and Mushrooms* **1**: 104-115, Adelaide 1934. The two European species indicated among the several Australian species, may be misdeterminations.

Those who do not arrive at satisfactory determinations with the help of the papers cited above, are advised that innumerable species have been described that are not considered in these keys. Karsten, Britzelmayr, and Velenovsky described numerous new species each, and these species have not come into general use, often rightly so because the species concept of these authors was a very narrow one, but also often wrongly since more detailed studies of the ana-

[159] It is perhaps worth while to indicate here that, according to the author's type studies, *Hebeloma verruculosum* Murr. [recte: *Cortinarius verruculosus* (Murr.) Sing.], *Hebeloma longisporum* Murr. [recte: *Cortinarius longisporus* (Murr.) Sing.], *Galerula Westii* Murr. [recte: *Cortinarius Westii* (Murr.) Sing.], *Inocybe Weberi* Murr. [recte: *Cortinarius Weberianus* Sing. n. n.], *Naucoria cuspidata* Murr. [recte: *Cortinarius cuspidatus* (Murr.) Sing.], *Naucoria mellipes* Murr. [recte: *Cortinarius mellipes* (Murr.) Sing.] and *Tricholoma iaganicum* (Speg.) Sacc. are *Cortinarii*.

tomy and the chemical characters of certain species show that these may be correlated with some minor macroscopical character emphasized by these authors. The same may be true of the twenty-four species of *Cortinarius* described by Murrill from Florida. Murrill's species are preserved at the University of Florida, and are accesible for further study.

125. LEUCOCORTINARIUS (Lange) Sing.

Lloydia **8** : 141. 1945.

Type species : Cortinarius bulbiger (A. & S. ex Fr.) Lange.

Syn : *Cortinarius* subgenus *Leucocortinarius* Lange, *Dansk Bot Ark* **8** (7) : 6. 1935.

Cortinellus Roze sensu Konr. & Maubl. *Icon. Sel. Fung* **6** : 146 1924-37 non sensu Karst (1879) nec sensu originali.

Characters : Those of *Cortinarius,* subgenus *Phlegmacium* sect. *Scauri* but spore print light ochraceous and spores smooth ; cuticle of the pileus consisting of interwoven hyphae which become more parallel in the epicutis ; pigment concentrated in the hypodermium, intracellular, or at least not incrusting the walls of the hyphae ; pileus neither distinctly viscid nor hygrophanous ; lamellae truncato emarginate ; hymenophoral trama regular ; spores under the microscope hyaline, rather thick walled (wall 0.5-1.0 μ thick), wall not distinctly double, without callus or germ pore, nonamyloid ; hyphae of the trama of the context interwoven, nonamyloid, consisting of hyphae with clamp connections. On the earth in woods.

Development of the carpophores : Unknown but probably as in *Cortinarius.*

Area : Europe.

Limits : This genus differs from *Tricholoma* (*Tricholomataceae*) in the somewhat thick-walled ochraceous spores, the cortina connecting the bulb with the margin of the pileus, the presence of clamp connections, which, in Tricholomas with even a trace of a cortina, are always constantly absent. *Leucocortinarius* differs from *Tricholomopsis* (*Tricholomataceae*) in the absence of cheilocystidia and in the presence of a bulb at the base of the stipe, also in more elongated spores and the color of the spore print. These differences would amply justify the generic separation of this genus from all similar forms in the *Tricholomataceae* but it is highly questionable whether they in themselves would be enough to remove *Leucocortinarius* from

Konrad & Maublanc and by Lange. Lange even went one step farther and considered *Leucocortinarius* as a subgenus of *Cortinarius,* an arrangement which the author thinks goes too far.

The author has, however, become convinced that Konrad & Maublanc and Lange were right in considering *Leucocortinarius* as belonging to the *Cortinariaceae* rather than the *Tricholomataceae.* This revision of the author's previous opinion is due to the cytological data given by Kühner in a recent paper (*Bull. Soc. Linn. Lyon,* 1945, n° 7-8, p. 160-169). Kühner says that the spores of *L. bulbiger* are binucleate which is contrary to what is usually found in the tricholomataceous genera, at least those that are similar to *Leucocortinarius.*

Within the *Cortinariaceae Leucocortinarius* can be distinguished easily by the combination of characters emphasized in the key and in the diagnosis.

State of knowledge : The characters of the only species kown are well established.

Practical importance : The genus may be of some importance in forestry since it seems to belong to the mycorrhizal fungi, more properly those that form ectotrophic mycorrhiza with conifers.

SPECIES

L. bulbiger (A. & S. ex Fr.) Sing. (Armillaria, Quel. ; Tricholoma, Ricken ; Cortinellus, Gillet ; Cortinarius, Lange).

125 a. DESCOLEA Sing.

Lilloa, 1951.

Type species : D. antarctica Sing.

Characters : Pileus ocher brown, the pigment incrusting the hyphal walls of the hypodermium, viscid, or with appressed floccons from the veil which forms a thin disappearing layer covering the epicutis ; velar layer consisting of hyphal bodies which are generally hyaline ; epicutis — a trichodermium which tends to become an epithelium because of the pressure of the velar layer during the young stages, i. e. the clavate bodies which are interwoven at places but generally appear to be erect, become short and ellipsoid to ovoid to globose and in many instances somewhat thick-walled ; lamellae emarginate or adnexed, narrow to broad ; spore print « buff » (Maerz &

Paul); spores under the microscope boat shaped, ventricose in the middle, below obliquely recurved into the hilar end, above mucronate-callose, with thick to very thick wall, distinctly to faintly punctate (exosporial ornamentation ?), with a well colored episporium and a pallid endosporium, acute on both sides, sometimes entirely smooth (especially when derived from bisporous basidia), rather large (more than 10 μ long), without germ pore and without suprahilar smooth spot (plage); basidia clavate, usually 4 spored, large; metuloids none; cheilocystidia making the edge of the lamellae heteromorphous, clavate cylindrical; cystidia on the sides of the lamellae none; trama of the hymenophore rather dense, regular, its hyphae strongly incrusted by pigment (rusty); stipe white, pale ochraceous or brownish, well developed and central, not bulbous-marginate at the base; veil well developed, membranous, forming a persistent annulus on the stipe; cortina none; all hyphae of the context with clamp connections. On the humus under *Nothofagus antarctica*, possibly forming mycorrhiza with it.

Development of the carpophores : hemiangiocarpous.

Area : Tierra del Fuego (Fireland).

Limits : Descolea differs from all other genera of the *Cortinariaceae* in the color of the spores, with the only exception of *Leucocortinarius*. This latter genus, however, differs strongly in the absence of an ornamentation on the spores, in the shape of the spores, in the different veil and the marginate base of the stipe. The structure of the epicutis is likewise very different, probably as a consequence of the development of the veil. It is true that, in the genus *Phaeomarasmius*, we know a few atypical species with rather pale, often ochraceous spore print, but these species are completely different from *Descolea* in epicuticular structure, in absence of sporal ornamentation, and in habit; they are never viscid, and their spores have a completely different shape. There does not appear to exist any close affinity to other genera of the *Cortinariaceae*, or at any rate not more affinity than the insertion in the same family would suggest.

State of knowledge : Only one species is known. Its macro- and microscopical characters have been studied completely, but the chemical characters are still unkown. It would also be interesting to know more about the relationship between this genus and the antarctic beech.

SPECIES

D. antarctica Sing.

126. **GYMNOPILUS** Karst.

Hattsv., Bidr. Finl. Nat. Folk. **32** : xxi. 1879.

Type species : G. liquiritiae (Pers. ex Fr.) Karst.

Syn. : ? *Rysospora* Fayod, *Ann. Sc. Nat., Bot.* VII. **9** : 361. 1889 (see also Sing. & Smith in *Mycologia* **38** : 284-285. 1946).
Fulvidula Romagnesi, *Rev. Mycol.* **1** : 209. 1936 ; nom. subnud.

Characters : Pileus usually bright colored, yellow, fulvous, red, blue, lilac, green, etc., the pigment incrusting the hyphal walls, viscid or hygrophanous, or dry, glabrous, fibrillose, squamulose, squarrose, floccose, or rimose; epicutis formed by hyphal chains which are frequently erect, forming some kind of a trichodermium, at least in the center of the pileus, and then the terminal members often assuming the character of dermatocystidia (e. gr. in *G. Zenkeri*), always incrusted by the pigment; lamellae adnexed to decurrent, narrow to broad, becoming very brightly and richly rusty in dried mature carpophores; spore print very brightly and richly ferruginous-fulvous, e. gr. « amber brown » with a slight shade of « Argus brown », or between « vinaceous orange » and « Mars orange », or brighter than « vinaceous russet » and « ferruginous » (Ridgway), between Pl. IV, A 12 and Pl. XI, A 12 or near « Arab » (Maerz & Paul); spores under the microscope usually well colored, rusty melleous, with double wall, without germ pore, ellipsoid, short-ellipsoid, or amygdaloid ellipsoid, distinctly warty when seen in ammoniacal medium under an oil immersion lens and focussed upon the upper surface (rather than in optical section); basidia either clavate or constricted between an apical capitate part and the lower ventricose part, or else ampullaceous, 4-spored or 2-spored; cystidia always present on the edge of the lamellae and in its neighborhood (cheilocystidia), sometimes this same type of cystidia found all over the sides of the lamellae, and then usually strongly incrusted with resinous pigment matter; cheilocystidia usually ventricose below, and the tapering apex often again thickened to a subcapitate tip, small to medium sized, scattered among the basidia or making the edge heteromorphous; hymenophoral trama regular; trama, subhymenium and hymenial elements

very frequently dyed uniformly deep and rich yellow because of a soluble (NH_4OH) intercellular (?) pigment permeating the preparation, consequently the hyphae becoming frankly green when dyed with some blues, e. gr. cotton blue C_4B according to Romagnesi (but it is not clear whether this behavior is also noticeable in the few species without yellow soluble pigment); stipe usually yellow or almost so, never considerably or constantly eccentric and always nearly as long as the diameter of the pileus or longer, well developed and not bulbous marginate, nor constantly strongly curved and thus touching the margin of the pileus, often with a distinct (cortinoid to membranous) veil which in some species appears as a well developed annulus, always annulate if the pileus is viscid, never showing a distinct pseudorrhiza but sometimes inserted in the wooden substratum; context often bitter; all hyphae with clamp connections. On coniferous wood, or on frondose wood, on dead palms, on living orchids, on grass roots, etc., rarely on foliage or other debris. The pileus becomes black with KOH especially when strongly dusted with the spores.

Development of the carpophores: Probably hemiangiocarpous in all species.

Area: Cosmopolitan.

Limits: The *Gymnopili* were confused by the mycologists with *Pholiota* (or what was then called *Flammula,* i. e. the non-scaly Pholiotas without annulus). The difference between these two genera is so obvious it is unnecessary to emphasize them. Yet, Romagnesi was the first author to distinguish methodically the *Gymnopili* from the *Flammulae,* and it is therefore regrettable that his genus *Fulvidula* has to be rejected for purely formal reasons in favor of Karsten's genus but the reasons for rejecting Karsten's genus as indicated by Romagnesi *l. c.* are not convincing. Since a type species had to be selected from the species originally included in *Gymnopilus,* one cannot see how it could have been avoided to choose a *Fulvidula.*

Gymnopilus is, as was already indicated by Romagnesi and Kühner, most closely related to *Cortinarius.* It can be distinguished from that genus by the correlation of the following characters: Bright color, bitter taste, lignicolous (or graminicolous) habitat in the cortinate forms (and these usually also green with cotton blue microscopically, and black with KOH macroscopically); the annulate forms differ from *Cortinarius* by this very character. The close relationship with *Cortinarius* is obvious enough, and has also found its expression

in the literature. Fries considered this group initially as a lignicolous section of *Cortinarius (Syst. Mycol.)*; Singer transferred one species to *Cortinarius*, only to reunite it subsequently with the *Flammulae* of the *Gymnopilus* group, and Patouillard described a *Flammula* which seems to be a *Cortinarius*. Nevertheless, the separation of *Gymnopilus* from *Cortinarius* has never caused any practical or theoretical difficulties. The line between the two genera is not under discussion, and the species belonging to them can be recognized by any-one who has understood the two types concerned, even without a microscope. *Gymnopili* can be easily grown on autoclaved media (Lutz's synthetic medium, malt agar); *Cortinarius* spp. do not grow under these conditions.

Another genus that is very close, is *Pyrrhoglossum*. The latter can be distinguished by the different habit. It is restricted to the tropics.

Under the name of *Crepidotus cacaophyllus* (Berk. & Curt.) Sacc., Saccardo describes a puzzling species from Cuba. The type in the Curtis Herbarium consists of only one specimen. It may be hoped that the Kew type is more copious. This species is indistinct and ordinary looking macroscopically but very interesting microscopically. There is on many hyphae a resinous incrustation of rusty chestnut color, and even the hymenial elements, even the spores, are unusually strongly incrusted. It seems that this is an abnormal form of a *Gymnopilus* whose normal propagation by basidiospores is partly inhibited by the excessive incrustation. It is impossible to tell what factors might have caused this strange behavior; excessively dry weather is only a guess; but the pallid color of the otherwise typical spores and the transformation of numerous basidia into cystidioles on the sides of the lamellae by a compact layer of resinous covering, making the formation of sterigmata impossible, tend to show that it is not a normally developed agaric. If this is so, there is no reason to assume that it is generically different from *Gymnopilus*. This became almost a certainty when an indubitable *Gymnopilus*, collected by the author in Florida during hot, rainless weather, turned out to have almost the same microscopical characters as *Crepidotus cacaophyllus*, only to a lesser degree. This specimen from Florida is identical with the South American *Gymnopilus peliolepis* (Speg.) Sing. *Crepidotus cacaophyllus*, if considered as an inhibited form of *Gymnopilus*, does not cause any difficulties in the delimitation of either *Crepidotus* or *Gymnopilus*, since it is evidently very distinct from all true *Crepidoti*, and definitely not or not much eccentric.

Another genus that may come close to *Gymnopilus* is *Phaeomarasmius*. Some species which the author has never studied personally, were recently mentioned by Romagnesi in a tentatively described genus « *Flavidula* ». This genus is said to differ from *Gymnopilus* by the smoothness of the spores which are otherwise identical with those of *Gymnopilus*. These species of « *Flavidula* » are undoubtedly very closely related to certain *Phaeomarasmii*, in fact Romagnesi does not make it quite clear how they differ. These *Flavidulae* have not been taken into consideration in the present work.

State of knowledge: After some special studies devoted to this genus, the species belonging here are comparatively well known. The whole subtropical and tropical group was revised recently by the author (ined.), but there are still certain species that are in need of more detailed data, especially some of the African forms. Several species of the temperate group growing on conifers are in need of revision. The number of species admitted here is 25 — but this number will greatly increase when more species are critically studied.

The subdivision into sections is rather difficult. Romagnesi's two sections, *Annulati* and *Cortinati* (= *Sapinei*) are here accepted but it must be realized that the veil may not in all cases be a character of primary importance.

Practical importance: None of the species of *Gymnopilus* has much economic importance at present. However, some of the species may occasionally be mild wood destroyers though they rarely infect freshly cut lumber. *G. aculeatus* seems to be an endotrophic mycorrhiza fungus of a tropical orchid. The yellow soluble pigment of many species is valuable as a dye for cytological work.

SPECIES

Sect. **1. ANNULATI** Romagnesi (1942 ut sectio *Fulvidulae* (= *Spectabiles* Konr. & Maubl. 1948 ut sect. *Pholiotae*). Membranous annulus persistent or cortina abundantly developed so as to form a distinct annulus.

Type species: *G. spectabilis* (Fr.) Sing.

G. janthinosarx (Sing.) Sing. (Fulvidula, Sing. 1937); *G. luteofolius* (Peck) Sing. (Pholiota, Sacc.); *G. dilepis* (Berk. & Br.) Sacc. (Flammula, Sacc.); *G. intermedius* (Sing.) Sing. (Pholiota, Sing. 1929; Cortinarius, Sing. 1936; Fulvidula, Sing. 1937); *G. aeruginosus* (Peck)

Sing. (Pholiota, Peck); *G. spectabilis* (Fr.) Sing. (Fulvidula, Romagnesi; Pholiota, Quel.; Pholiota ventricosa Earle; Gymnopilus annulatus Murr.); *G. suberis* (R. Maire) Sing. (Fulvidula, Sing.; Pholiota, R. Maire); *G. pampeanus* (Speg.) Sing. (Pholiota, Murr.; Flammula Brittoniae Murr.; Flammula Eucalyptorum Cleland [27]); *G. aculeatus* (Bres. & Roumeguère) Sing. (Pholiota, Bres. & Roumeguère); *G. peliolepis* (Speg.) Sing.; probably also the following species: *G. purpuratus* (Cooke & Mass. sensu Cleland) Sing. (Agaricus purpuratus Cooke & Mass.), *G. Braendlei* (Peck) Sing (Flammula, Peck), *G. pulchrifolius* (Peck) Murr. (Flammula, Peck), and *G. imperialis* (Speg.) Sing. (Pholiota, Speg.)

Sect. 2. **SAPINEI** (Fr. ut sectio *Agarici* trib. *Flammulae*) Sing. (= *Cortinatae* Romagnesi, 1942 ut sectio *Fulvidulae*) Veil slight, consisting of fine fibrils or a cortina, rarely forming an annulus, often practically absent.

Type species : G. sapineus (Fr.) R. Maire.

G. punctifolius (Peck) Sing. (Cortinarius, Peck; Flammula, A. H. Smith; Flammula subviridis Murr.); *G. bellulus* (Peck) Murr. (Naucoria, Sacc.; Flammula, Kühner; Fulvidula, Kühner); *G. sapineus* (Fr.) R. Maire (Flammula, Quél.; Fulvidula, Romagnesi); *G. penetrans* (Fr. sensu Lange) Murr. (Flammula, Quel. sensu Lange non Bres. which = G. hybridus); *G. hybridus* (Fr. ex Fr.) Sing. [Flammula sapinea var. hybrida (Fr.) Konr. & Maubl.; Fulvidula hybrida Romagnesi]; *G. amarissimus* Murr. with its var. *subdryophilus* Murr. (ut sp., ined.); *G. liquiritiae* (Pers. ex Fr.) Karst. (Flammula, Quél.; Fulvidula, Romagnesi); *G. microsporus* (Sing.) Sing. (Fulvidula, Sing.; Flammula liquiritiae sensu Bres. non Fr.); *G. picreus* (Fr.) Karst. (Flammula, Gillet; Fulvidula, Sing.); *G. alpinus* (Sing.) Sing. (Fulvidula, Sing.); *G. tonkinensis* (Pat.) Sing. (Tubaria, Pat.); *G. fulgens* (Favre & Maire) Sing. (Naucoria, Favre & Maire; Fulvidula, Kühner); *G. flavus* (Bres.) Sing. (Naucoria, Bres.; Fulvidula, Sing.; Flammula dactylidicola Lange; Fulvidula, Sing.); *G. chrysopellus* (Berk. & Curt.) Murr. [Flammula, Sacc.; probably identical: *G. chrysotrichus* (Berk. & Curt.) Murr. and *G. aureobrunneus* (Berk. & Curt.) Murr.]; *G. Zenkeri* (Henn.) Sing. (Flammula, Henn.); *G. praefloccosus* Murr.

Note : There are many more species of the genus *Gymnopilus* in the American literature. While it is obvious that they belong in this

[27] The two latter, *G. suberis* and *pampeanus*, are probably geographical races of *G. spectabilis*

genus, their relationship with other species cannot be considered cleared up enough to assign them a place in the classification of the genus. These species are :

G. flavidellus Murr. ; *G. oregonensis* Murr. ; *G. echinulisporus* Murr. ; *G. chrysotrichoides* Murr. ; *G. palmicola* Murr. ; *G. pholiotoides* Murr. ; *G. parvulus* Murr. ; *G. hispidellus* Murr. ; *G. subpenetrans* Murr. ; *G. Earlei* Murr. *G. depressus* Murr. ; *G. tenuis* Murr. ; *G. areolatus* Murr., and probably several more species.

There are also many species from Africa (aside from *G. aculeatus* and *G. Zenkeri*), and from European greenhouses. All these species are not considered in the following key.

KEY TO THE SPECIES

A Stipe with a distinct annulus at beginning maturity.

B Context or apex of the stipe « light purplish vinaceous » (Ridgway), or some similar bright color ; pileus often rose or red on the scales, often areolate ; on frondose trunk in North America. *G. luteofolius*

B. If there is any vinaceous color in the carpophores, the habitat is not on frondose trunks in North America but on various trunks in Asia.

C Context lilac-violet ; pileus somewhat viscidulous. On coniferous trunks in Central Asia (Katun river) *G. janthinosarx*

C Context usually not lilac-violet ; pileus usually not viscidulous, and never combining both these characters.

D. Context of the pileus reddish or greenish ; pileus with aerugineous spots on reddish ground or vice versa, or entirely greenish, in the Caucasus or in North America.

E. Pileus reddish with aerugineous spots ; context of the pileus reddish ; on trunks of *Carpinus*, *Castanea* and other frondose trees in the Caucasus. *G. intermedius*

E. Pileus mainly aerugineous, sometimes reddish as well as aerugineous ; context of the pileus greenish ; on trunks of frondose and coniferous trees, e. gr. *Quercus* and *Thuja*, also on railway ties in North America. *G. aeruginosus*

D Context of the pileus white (at least when young), or yellowish to fulvous (especially when old) ; pileus not so colored.

F. Pileus with some bluish violet or greenish spots, or entirely violet-blue in youth. Indo China, perhaps also on Ceylon, Java, etc. *G. dilepis*

F Pileus yellow to fulvous, or purple red, never with any bluish or violet, or greenish tints in fresh condition.

G Pileus rather large and fleshy in most normally developed specimens, with innately squamulose-fibrillose suface or slightly rimose, sometimes merely innately

palms, not known from *Eucalyptus*), mainly in the temperate zones. *G. spectabilis*

G. Pileus either with individualized scales that are often erect (squarrose) on the disc, or at least not innately fibrillose, or else the species is tropical, or it grows exclusively on *Eucalyptus* or on palms.

H. On *Quercus* in North Africa. *G. suberis*

H. Usually on other frondose trees (*Eucalyptus*), or on palms, or not bitter.

I. Pileus with red scales at least when young

J. Cheilocystidia capitate (at least the vast majority of these elements); on *Monocotyledones* in Florida, West Africa, etc. *G. aculeatus*

J. Cheilocystidia fusoid or ampullaceous (at least their majority); on frondose trees (*Dicotyledones*) in North to South America (tropical and subtropical belt). *G. peliolepis*

I. Pileus without red scales, scales of young and fresh specimens either concolorous (yellow) or fulvous to brown.

K. All cheilocystidia ampullaceous or fusoid; also some pleurocystidia which are strongly incrusted and otherwise identical with the cheilocystidia present; taste mild. On frondose trees in Florida and the West Indies, also in South America. (see *G. chrysopelius*)

K. Not combining all these characters. On frondose trees, most frequently *Eucalyptus*. In South America, Australia, etc. (if on palm in subtropical or tropical America, cf. *G. aculeatus*). *G. pampeanus*

A. Stipe not or not distinctly annulate.

L. Pileus pink, or latericious, or partly so (see « B », cf. *G. pulcherifolius*).

L. Pileus not so colored

M. Pileus bluish green or yellowish green; context greenish. North America. *G. punctifolius*

M. Not so colored

N. Carpophores growing directly on dead wood, or on buried wood, or on the base of trees or stumps, usually gregarious, more rarely solitary, sometimes on fallen twigs or on cones of conifers.

O. On Coniferae

P. Pileus usually squamulose with innate fibrillose scales, or with hairy scales on the disc

Q_1 Pileus usually with innate, fibrillose scales, or merely fibrillose subglabrous. *G. sapineus* and *G. bellulus* [421]

Q_2 Scales hairy or fibrillose-squarrose, mainly conspicuous on the disc. (see *G. chrysopeplus*)

P_2 Pileus glabrous.

R_1 Pileus non hygrophanous, or merely with a hygrophanous margin in occasional thin specimens; context of stipe not entirely brown in fresh, young specimens.

S_1 Cheilocystidia all or almost all ampullaceous, not capitate. Temperate species. *G. penetrans*

S_2 Cheilocystidia mostly capitate.

T_1 Large carpophores with well developed veil. Temperate species. *G. hybridus*

T_2 Carpophores of varying size, practically without veil. Warmer parts of North America. *G. amarissimus*

T_3 Small carpophores; northern and mountain regions, see U_2.

R_2 Pileus hygrophanous, thin, splitting, striate on the margin when old; context of the stipe entirely brown when old and when young.

U_1 Spores 8 µ or longer.

V_1 Stipe glabrous, fulvous ferruginous; lamellae broad, somewhat ventricose. Mostly on *Abies* in Europe and Northern Asia, also in North America. *G. liquiritiae*

V_2 Stipe pruinate when young, rather dark brown; lamellae narrow, not ventricose. Temperate species. *G. picreus*

U_2 Spores smaller. Mountain forests (mostly on *Abies*) in Europe and in the Caucasus. *G. microsporus* (cf. *G. bellulus* sensu Kühner)

O_2 On frondose wood.

W_1 Pileus covered all over with small floccose squamules, squarrulose on the disc; spores very small (5.8-6.5

[421] *G. bellulus* belongs in the difficult *G. sapineus* group which is still in need of more special studies. Fries' original *A. sapineus* grows on *Picea abies*, rarely on *Pinus silvestris* in Northern Europe and is a large fleshy species. Smaller species, among others *F. bellulus*, have often been confused with *G. sapineus* in the narrower sense. The present interpretation of *G. bellulus* is based on an authentic specimen in the Burt Herbarium. But see also Kühner's interpretation based on non-authentic material. (*Quelques Agarics rares ... de la region de Besançon*, p. 15, without year).

× 4-4.8 μ ; cheilocystidia ampullaceous. Tropical West Africa. *G. Zenkeri*

W. Pileus with a different covering ; spores usually somewhat larger ; cheilocystidia either ampullaceous or capitate. Not known from Africa (but species corresponding to this characterization may occur there).

X. Pileus scaly, the scales either yellow or fulvous or brown or red ; cheilocystidia ampullaceous to fusoid, often also ocurring on the sides of the lamellae (« pleurocystidia ») in young carpophores ; taste mild ; subtropical and tropical North, Central and South America. *G. chrysopellus*

X. Not combining all these characters ; cheilocystidia capitate. Florida.

Y. Pileus glabrous, or more rarely with some partly erect fibrils ; taste extremely bitter. *G. amarissimus* var. *subdryophilus*

Y. Pileus covered with conspicuous erect spines, very strongly echinate-shaggy ; taste somewhat astringent. *G. praefloccosus*

N. Carpophores growing on the earth or humus or small rotten sticks, often on the roots or decaying stems of grasses, on decaying foliage, etc.

Z. Spores 6.6-10 μ long, mostly 8-9 μ long.

AA. Alpine species of the Caucasus Mts. on alpine meadows. *G. alpinus*

AA. Small species occurring on peat-soil among *Polytrichum* in Europe, or on forest humus (with leaf-debris) in Indo-China.

BB. Lamellae broad and decurrent ; on decayed fragments of foliage and small sticks on the ground in the forest. Indo-China (Tonkin). *G. tonkinensis*

BB. Lamellae rather broad but emarginate adnate or sinuate-adnate, or plainly adnate, not decurrent. Europe (French Jura). *G. fulgens*

Z. Spores 5-6 (7.5) μ long. On *Dactylis glomerata*, from Denmark to Italy and west to Spain. *G. flavus*

127. PHAEOCOLLYBIA Heim

Genre Inocybe, p. 70. 1931.

Type species : Naucoria festiva (Fr.) Bres.

Characters : Habit collybioid ; pileus usually glabrous, humid subviscid to glutinous, often acute, conical to campanulate, later expanding and often umbonate ; epicutis consisting of repent, filamentous

hyphae which are more or less gelatinized or at least not tightly packed; lamellae subfree to narrowly adnexed, becoming rusty brown to deep and rich cinnamon color in age, with paler edge (use a lens); spore print rusty; spores rusty to rusty melleous (rusty and well colored if strongly warty, more melleous when less ornamented), ornamentation warty but sometimes almost subsmooth, without plage, without germ pore and callus, ellipsoid to ovoid subamygdaliform; basidia normal; cystidia none on the sides of the lamellae but always present on the edges of the lamellae, narrow, filamentous-capitate, making the edge more or less heteromorphous; hymenophoral trama regular with densely packed subparallel hyphae; stipe cartilaginous but often fragile, especially in dried condition, innately striate-fibrillose or more frequently quite smooth; pseudorrhiza more or less developed and often very conspicuous; veil rudimentary, pruinose, practically absent even in young specimens; all hyphae with clamp connections. On earth and humus, and on rotten wood, mostly in coniferous woods and possibly rising from some buried vegetable matter which is reached by the pseudorrhiza.

Development of the carpophores. Unknown.

Area: Temperate zone (circumpolar).

Limits: The absence of a cortina and the characters of the stipe separate this genus from *Cortinarius*. In the latter genus, it would be looked for in *Phlegmacium*. In that subgenus, however, all species are stouter and fleshier. *Phaeocollybia* differs from *Gymnopilus* in the combination of a viscid pileus and an evelate stipe, also in the more developed pseudorrhiza, and in the narrowly adnexed to subfree lamellae. It differs from *Galerina* in the combination of clamped hyphae and spores without plage, also in the colors.

State of knowledge: Thanks to recent studies by several authors (Heim, A. H. Smith, and others), the species belonging to this genus are reasonably well known.

Practical importance: None.

SPECIES

P. festiva (Fr.) Heim ex Sing. (Naucoria, Bres.); *P. Christinae* (Fr.) Heim (Naucoria, Quél.); *P. lugubris* (Fr.) Romagnesi (Naucoria, Quél.); *P. hilaris* (Fr. sensu Ricken) Romagnesi (Naucoria, Quél.); *P. cidaris* (Fr.) Romagnesi (Naucoria, Sacc.; Naucoria Jenniae Karst.; Phaeo-

collybia, Romagnesi); *P. Kauffmanii* (A. H. Smith) Sing. (Naucoria, A. H. Smith); *P. attenuata* (A. H. Smith) Sing. (Naucoria, A. H. Smith); *P. similis* (Bres.) Sing. (Naucoria, Bres.); *P. radicata* (Murr.) Sing. (Naucoria, Sing.), also *P. hamadryas* (Fr. sensu Cooke) according to Heim.

KEY TO THE SPECIES

A. Spores distinctly warty.
- **B. Spores 7 µ or longer.**
  - **C. Pileus 80-195 mm broad; spores reaching 10 × 6 (7) µ. From Washington to California.** *P. Kauffmanii*
  - **C. Pileus 15-100 mm broad; spores reaching 9 × 7 µ.**
    - **D. Spores short, 7-9 × 6-7 µ. China (Yunnan).** *P. similis*
    - **D. Spores more oblong.**
      - **E. Pileus usually olive or green; stipe often violet; lamellae dusky violet or olive or red; stipe tubular. Europe and American West.** *P. festiva*
      - **E. Pileus, stipe and lamellae differently colored; stipe sometimes stuffed at first.**
        - **F. Pileus acutely conical, 30-100 mm broad; stipe 80-200 mm long, always strongly radicant, 6-20 mm thick. Europe and North America.** *P. lugubris*
        - **F. Pileus campanulate, then obtuse, 17-48 mm broad; stipe only 3-5 mm thick and pseudorrhiza often inconstant.**
          - **G. Stipe striped, fibrillosely dissolving, fragile, up to 60 mm long; odor farinaceous. Europe.** *P. hilaris*
          - **G. Not combining the characters indicated above; odor raphanoceous. Washington to California.** *P. attenuata*
- **B. Spores 6 µ long or shorter.**
  - **H. Pileus distinctly viscid.** *P. Christinae*
  - **H. Pileus subviscid.** *P. cidaris*

A. Spores indistinctly rough. *P. radicata*

128. PYRRHOGLOSSUM Sing.

Mycologia 36: 367. 1944.

Type species: *Agaricus pyrrhus* Berk. & Curtis.

Characters: Habit pleurotoid; pileus sublaterally or strongly eccentrically attached with or without a stipe; epicutis made up of elongate, more or less repent hyphae, many of the cuticular hyphae incrusted by a membrana pigment (chestnut to melleous); lamellae eventually becoming bright rusty colored; spore print bright rusty;

spores small, distinctly warty without germ pore and callus, with a rich rusty color at least in the ornamentation; basidia normal; cystidia none on the sides of the lamellae but cheilocystidia always present, ampullaceous or filamentous capitate; trama of the lamellae regular, its hyphae not gelatinized, colored bright and deep lemon yellow by a soluble (in ammonia) fast diffusing pigment that permeates the whole preparation (as in *Gymnopilus, Pleuroflammula, Omphalotus, Pulveroboletus,* etc.); stipe either practically absent (very reduced and appressed, having lost its function, thin and short and oblique or strongly curved), or strongly eccentric and oblique and shorter than the diameter of the pileus; veil inconspicuous or none; all hyphae with clamp connections. On wood.

Development of the carpophores: Unknown.

Area: Tropics, and in parts of the southern hemisphere (Florida to Chile, and West Africa).

Limits: The pleurotoid habit of the carpophores separates this genus from all genera of the *Cortinariaceae.* The warty spores and smaller cheilocystidia separate it from *Pleuroflammula.* The rusty spores without germ pore separate it from *Melanotus.*

Pyrrhoglossum is undoubtedly closest to *Gymnopilus.* With this latter genus it shares all the essential characters, and even the bright yellow soluble pigment, and the KOH reaction. The structure of the trama and epicutis is also the same in both genera, and the substratum is identical in *Pyrrhoglossum* and the majority of the species of *Gymnopilus,* viz. decaying wood. It is divided from *Gymnopilus* by a definite hiatus. This hiatus, mainly expressed in the difference in habit, is accentuated by the difference in the geographic distribution which is rather limited in *Pyrrhoglossum,* and cosmopolitan in *Gymnopilus.* It also appears that the spores are always small in *Pyrrhoglossum* and the warts comparatively more strongly developed and more contrasting with the episporium.

State of knowledge: The two species belonging here are well known.

Practical importance: None.

SPECIES

P. pyrrhus (Berk. & Curt.) Sing. (Agaricus, Berk. & Curt.; Crepidotus, Sacc.); ***P. stipitatum*** Sing.

129. **GALERINA** Earle

Bull. N. Y. Bot. Gard. **5** : 423. 1909

Type species : Agaricus vittaeformis Fr., Epicrisis.

Syn. : Galera (Fr.) Quél., *Champ. Jura Vosges*, p. 135. 1871-72, non Blume (1825).
Agaricus tribus *Galera*, Fries, *Syst. Myc.* **1** : 264. 1821.
Pholidotopsis Earle, *Bull. N. Y. Bot. Gard.* **5** : 443. 1909.
? *Galerula* Karst., *Bidr. Finl. Nat. Folk* **32** : xxiii. 1879, p. p. (genus incertae sedis).

Characters : Habit usually mycenoid, but sometimes collybioid or omphaloid and sometimes fleshier than usual and with well developed veil (these fors have formerly been mistaken for *Pholiota*); pileus usually more or less hygrophanous usually campanulate or conical in the early stages, but occasionally also semiglobose or bullate, with an epicutis of strictly repent hyphae (some may at places have suberect ends but no palisade or hymenium is ever formed); dermatocystidia rare and inconstant on the pileus, usually absent, globose cells none in the cuticle; pigment incrusting, melleous to brownish chestnut, tawny, ochraceous, etc. rarely green or blue, or red; lamellae adnexed to decurrent, usually white fringed; spore print more or less richly rusty in color (e. gr. « Alamo » - Maerz & Paul); spores under the microscope melleous to rusty-fulvous, often rather pale colored in water or chloralhydrate but becoming richly and deeply rusty in alkalis, rarely smooth, usually with some kind of ornamentation which may be very low, or else very distinct and projecting and then usually distinctly warty or in short ridges, sometimes the ornamentation supplemented or replaced by a perisporial ornamentation (Pl. XI, 1), the walls distinctly complex, without a germ pore but sometimes with a distinct callus, with a plage, i. e. with a suprahilar smooth disc on the inner side of the spore (Pl. XII, 3), rarely without it, and then the hyphae without clamp connections; basidia normal but either 4-spored, or 2-spored (or mixed), also many monosporous and trisporous basidia observed in some species; cystidia often present, in some species constantly present on the sides of the lamellae, in others only cheilocystidia present, but the latter never absent : hymenophoral trama regular or subregular, not bilateral in any sense : hymenopodium little developed; stipe with traces of a cortinoid veil, more rarely practically

evelate, and often with a distint annulus which is membranous and usually whitish; dermatocystidia numerous only in one species; mycelium whitish; in deep moss, especially *Sphagnum*, but also in other moss beds, among herbs (mostly grasses), on humus (mixed with needles, foliage, wooden debris), on sandy earth or loam, on dead branches, stumps, logs, or dead bark of dead or living trees, etc.

Development of the carpophores. Probably always hemiangiocarpous.

Area : More common in the boreal zone than in the other zones, very rare in the tropics but not entirely absent.

Limits : The presence of a plage on the spores (unless clamp connections are absent), in connection with an epicutis of repent hyphae and a rusty spore print always clearly defines a species as belonging to this genus. The only difficulty may be encountered in such species where the ornamentation is so indistinct or perhaps lacking that the plage cannot be observed with certainty. These latter species have much thicker spore walls than the species of *Tubaria* or *Phaeomarasmius* that might possibly be confused with them, and the endosporium and episporium are quite distinctly discernible and the epicuticular hyphae are repent. In this category belong *G. macrospora* and *G. paludosa*; perhaps also *G. clarus* Romagnesi.

Agaricus helvoliceps Berk. & Curt (the portion of the type preserved in the Curtis Herbarium [21]) has been suspected by the author to belong in *Alnicola* from which it differs in the pleurocystidia, or in *Galerina* from which it differs in the color of the spore print. The print has been preserved with the specimens and appears to be rather sordid brown than ferruginous. However, when the spore dust is removed from the paper, and compared with equally old prints of *Galerina*, there is hardly any difference noticeable. This observation is confirmed by the fact that specimens collected by W. H. Tranzschel in the greenhouses of the Botanical Garden in Leningrad, and then determined as *Galerina Tranzschelii* Sing. in sched. (ined.), are identical with the Curtis type of *Agaricus helvoliceps*. This means that the latter should be transferred to *Galerina* where it comes closest to *G. marginata* and related species.

Such tropical marasmioid species as *Galerina sulcipes* (Berk.) Sing. (Marasmius, Berk.; Phaeomarasmius, Boedijn) certainly belong in the genus, but the section is doubtful.

[21] Strangely enough, the specimens in the Patouillard Herbarium are not in the least similar to those of the Curtis Herbarium. They belong in *Deconica*

State of knowledge : The Galerinas are well known. This is mainly due to the fact that special studies have been devoted to them in North America (Atkinson) as well as in Europe (Kühner). It is now obvious that the genus *Galerina* consists of species formerly scattered all over the genera of the rusty spored agarics (*Pholiota, Flammula, Naucoria, Galera, Tubaria,* and even *Inocybe*). It contains at least 20 species, i. e. 20 species are completely known at present.

Practical importance : Some of the species may be of some interest for geobotanists since they are always found in very definite associations, and seem to characterize some of the various types of sphagnose woods and Sphagneta. One species in the tropics (*G. sulcipes*) and perhaps one in North America (*Pholiota autumnalis*) are poisonous.

SPECIES

Sect. 1. **TUBARIOPSIS** Kühner (1935). Plage absent ; clamp connections absent, at least in the covering layers.

Type species : G. graminea (Vel.) Kühner.

G. graminea (Vel.) Kühner ; *G. clavata* (Vel.) Kühner (both species described as *Galera* by Velenovsky).

Sect. 2. **EU-GALERINA** Kühner (1935), em. Plage of the spores present unless the spores are virtually smooth ; clamp connections present in the covering (cortical) layers of the pileus and stipe ; cystidia on the sides of the lamellae none, or few, and then pileus very fragile, conico-campanulate at first.

Type species : G. Hypnorum (Schrank ex Fr.) Kühner.

Stirps **Sphagnorum** (Among *Sphagnum*).

G. Sphagnorum (Pers. ex Fr.) Kühner (sensu Atk.) (Galera, Karst.) ; *G. tibiicystis* (Atk.) Kühner (Galerula, Atk.) and *Galerula lasiosperma* Atk. which is identical with the preceding species according to Kühner ; *G. paludosa* (Fr.) Kühner (Galera, Quél. ; Tubaria, Karst.) with a broad-spored American subspecies which may be *Galerula sphagnicola* Atk ; *G. stagnina* (Fr.) Kühner (Galera, Quél. ; Tubaria, Gillet) ; *G. macrospora* (Vel.) Sing. (Galera, Vel.).

Stirps **Mycenopsis** (Not among *Sphagna* ; spores virtually smooth).

G. mycenopsis (Fr. sensu Ricken) Kühner (Galera, Quél. ; Naucoria, Schroter).

Stirps **Hypnorum** (Usually not among *Sphagna*, often evelate or

with slight veil; spores either distinctly warty or with persistent perisporium).

G. mniophila (Lasch) Kühner (Galera, Gillet); *G. Hypnorum* (Schrank ex Fr.) Kühner (Galera, Quél.) with several varieties.

Stirps **Triscopa** (Not among *Sphagna*, often on wood, or with strongly developed veil; spores distinctly rough, or at least with a distinct plage).

G. mycenoides (Fr. sensu Jaap) Kühner (Pholiota, Quél.; Galera, Quél. 1886); *G. triscopa* (Fr.) Kühner (Naucoria, Quél.); *G. pseudocamerina* Sing. [Galerina camerina (Fr. sensu Quél.) Kühner non Agaricus camerinus Fr.]; *G. sideroides* (Fr.) Kühner sensu Kühner (Naucoria, Quél.); *G. uncialis* (Britz.) Kühner (Galera, Sacc.).

Sect. 3. **NAUCORIOIDES** Kühner (1935), em. Pleurocystidia always present; clamp connections always present; veil often well developed and annulate; pileus often very obtuse at least at maturity, or else stipe beset with numerous dermatocystidia.

Type species : G. marginata (Batsch ex Fr.) Kühner.

Stirps **Rubiginosa** (Stipe pubescent because of the dermatocystidia).

G. rubiginosa (Pers. ex Fr.) Kühner sensu Kühner [Galera, Gillet; G. Hypnorum var. rubiginosa (Pers. ex Fr.) Quél.; A. vittaeformis Fr. (sensu Ricken); Galera, Quel., Ricken]; also *G. muricellospora* (Atk.) Kühner (Galerula, Atk.) which is but a bisporous form of the preceding species.

Stirps **Marginata** (Stipe strongly veiled, annulate, or at least not pubescent; cystidia of the *Inocybe*-type absent).

G. marginata (Batsch ex Fr.) Kühner (Pholiota, Quel.); *G. helvoliceps* (Berk. & Curt.) Sing. (Flammula, Sacc.); *G. unicolor* (Vahl in Fl. Dan. ex Fr.) Sing. (Pholiota, Gillet.; *G. cedretorum* (R. Maire) Sing. (Galerula, Maire); *G. paludicola* (Atk.) Sing. (Galerula, Atk.), at least in the author's interpretation.

Stirps **Nana** (Cystidia thick walled and reminiscent of the muricate pleurocystidia of *Inocybe*).

G. nana (Petri) Kühner (Naucoria, Petri).

KEY TO THE SPECIES

The excellent monograph of the « *Galerae* » published by Kühner in 1935, and an earlier paper by Atkinson on « *Galerula* » can both be used for the identification of the Galerinas. Some additional species described since then by Favre, Romagnesi, and others, and some binomials that must be changed for nomencla

torial reasons [133] must be inserted and substituted for names adopted by Atkinson and Kühner (for citations see « Literature »).

130. PHAEOMARASMIUS Scherffel

Hedwigia **36** : 289, 1897, em.

Type species : *P. excentricus* Scherffel.

Syn. : *Marasmiopsis* Henn. in Engl. & Prantl, *Nat. Pfl.-fam.* **1** (1**) : 230, 1898.
Flammulaster Earle, *Bull. N. Y. Bot. Gard.* **5** : 435, 1909.
Epicorticium Vel., *Mykologia* **3** : 72, 1926.

Characters : Habit collybioid-marasmioid and often somewhat pleurotoid, or else collybioid; pileus non viscid and more frequently non hygrophanous than hygrophanous, beset with small punctations, floccons, or squamules of a covering layer which is deep and richly colored (fulvous rufous, etc.), or else evenly subvelutinous or furfuraceous and glabrescent; epicutis an (often disrupted) trichodermium palisade, the terminal members of the hyphal chains mostly dermatocystidioid, or many of the members very strongly shortened, with an epithelium-like structure resulting, mostly incrusted by pigment; pileus at first convex, often semiglobose, margin often sulcate; lamellae adnate to subfree, distant or subdistant, more rarely subclose, always with pallid edge when fresh and seen under a lens; basidia normal but often bisporous, cystidia on the sides of the lamellae none, or rarely scattered cheilocystidia reaching part way up from the edges which are heteromorphous; cheilocystidia always present, conspicuous; spores in print from as light colored as « Nankeen » to between « spruce yellow » and « Inca gold » (Maerz & Paul), or reaching Ségny 336, between « burnt umber » and « Alamo », or from « Arab » to « Cognac » (Maerz & Paul); spores rusty melleous rarely subhyaline under the microscope, always perfectly smooth, with a callus but without germ pore, with double wall but wall not extreme-

[133] The author has used as much as possible the nomenclature proposed by Kühner. However, in a few cases, the epithet used by Kühner is untenable for strictly nomenclatorial reasons. Since Kühner says that his *Galerina badipes* is not that of Fries, he cannot use Fries' name inasmuch as there is a good recent name available. The same goes for his *G. camerina*. Since he indicates *Agaricus camerinus* as being the same as *G. cedretorum* (R. Maire) Kühner, it is obviously not in accordance with the rules to maintain an independent and different spe-

ly thick, shape varying according to the species and to specimens, from subreniform-ellipsoid to subamygdaliform-ellipsoid, or ellipsoid to ellipsoid oblong or somewhat cylindric; hymenophoral trama regular; stipe rather thin, or medium thick, fragile to rather tough but not truly cartilaginous, with a slight to distinct veil, and in many species even subannulate to annulate, without pseudorrhiza, often slightly eccentric and often comparatively short in the wood inhabiting forms; all hyphae with clamp connections. On the earth on débris of various plants, or, more frequently on fallen sticks, logs, or stumps, or on dead or living cortex of frondose trees, rarely among moss.

Development of the carpophores: Unknown, probably always hemiangiocarpous.

Area: Unknown. Certainly occurring in Europe and Siberia, North America, and South America.

Limits: The limits of this genus are difficult to establish at the present time. Originally, this genus was confined to such species that had a somewhat marasmioid habit; later the thick-walled elements with their strong incrustation as observed in *P. aridus* and *P. horizontalis*, in Europe, and *P. rufolateritius* and *P. distans* in North America, were emphasized by Kuhner (1935, and Singer (1936), but several years later, Romagnesi stated his opinion that all the Naucorias (i. e. species of *Naucoria* in the narrower sense proposed by Singer 1936) must have hygrophanous pileus and dermatocystidia on the pileus rather than a cellular covering of pileus and stipe and non hygrophanous pileus. The latter species, such as *N. Wieslandri*, were transferred by Romagnesi to a group of ochrosporus agarics which he refrained from naming but indicated as being very close to *Phaeomarasmius*, so close indeed that this latter genus cannot any more be considered as isolated. This opinion of Romagnesi's is here accepted, and the species excluded by him from *Naucoria* sensu stricto are included in *Phaeomarasmius*.

If *Phaeomarasmius* is interpreted in this somewhat broader sense, several problems of delimitation will arise. The three most important ones are:

(1) Delimitation of *Phaeomarasmius* against *Naucoria* sensu stricto. If all the non hygrophanous species are removed from *Naucoria*, this does not mean that all the species of *Phaeomarasmius* must be non hygrophanous. *Naucoria confragosa* (Fr.) Sing. which was formerly

as a *Tubaria* by Kühner, are actually hygrophanous, as also correctly indicated by Fries. These species have spores of the character of those of *Naucoria* and *Phaeomarasmius* rather than *Tubaria* or *Pholiota*. The subfree lamellae and the epithelium isolate *N. carpophila* completely from *Tubaria* with which, undoubtedly, it is not closely related. If it is regarded as a *Phaeomarasmius*, it joins its nearest relatives which, in the author's opinion, are *P. granulosus* and *P. siparius*. *Naucoria confragosa* is likewise closer to *Phaeomarasmius*. It has the veil, the spore color and the pigment incrustation in the epicutis to separate it from *Naucoria* in the new restricted sense.

(2) Delimitation of *Phaeomarasmius* against *Gymnopilus*. The species personally known to the author do not appear to make a discussion of the separation of *Phaeomarasmius* from *Gymnopilus* necessary. The two genera are well separated by the spores which are either ornamented (in *Gymnopilus*) or smooth (in *Phaeomarasmius*). The only species of *Phaeomarasmius* with spores other than smooth, viz. *P. monticulus* (Henn.) Sing. is not brown spored at all since the spores described by Pilát are mold spores. The basidiospores of this species are hyaline and smooth. It belongs to *Crinipellis*. *Phaeomarasmius confragosus* was likewise inserted in *Gymnopilus (Fulvidula)* by an erroneous interpretation of old notes by this author. It was subsequently transferred to *Naucoria* where it belongs according to the author's original interpretation of the genus *Naucoria* (see also above).

Romagnesi indicated a group of species which can be characterized as smooth spored *Gymnopili*. If such a group exists and is actually close to *Gymnopilus*, this would indicate a much closer affinity between *Phaeomarasmius* and *Gymnopilus* than was suspected formerly. However, Romagnesi compares his group — he calls it *Flavidula* (ad interim) — with *Flammula* (i. e. *Pholiota* p. p. in the present classification) rather than with *Gymnopilus*.

(3) Delimitation of *Phaeomarasmius* against *Pholiota*. If Romagnesi's *Flavidula* is actually close to *Pholiota*, perhaps as a group without chrysocystidia, but otherwise comparable with *Pholiota* sect. *Squarrosae*, this would mean that a group of this character is intermediate between *Phaeomarasmius* and *Pholiota*. In this case, the delimitation of *Phaeomarasmius* and *Pholiota* becomes very urgent and important because it may in the end have a bearing on the final position of the former genus, in the *Strophariaceae* or in the *Cortinariaceae*. If « *Flavidula* » is disregarded, the genus *Phaeomarasmius*

differs from *Pholiota* in size and habit, in spores with callus rather than with germ pore, in the absence of chrysocystidia or if the sections of *Pholiota* without chrysocystidia are considered in a different structure of the epicutis (the scales either made up of appressed fibrils, or else epicuticular hyphae gelatinized in the Pholiotas).

A more profound study of the « *Flaridulae* » and such species as may appear close to them, and furthermore, all the smaller Pholiotas without chrysocystidia, appears to be necessary in order to be certain of the delimitation outlined above. The author does not take these species into immediate consideration because they are described without indication of a few important characters, besides, they are not at all known to the author from personal experience. Without farther study of the delimitation of the genus *Phaeomarasmius* from the genus *Pholiota*, the insertion of the former among the *Cortinaciaceae* must be considered as merely tentative. If transferred to the *Strophariaceae*, the genus *Phaeomarasmius* would be intermediate between *Pholiota* and *Kuehneromyces*.

(4) Delimitation from *Cystoderma*. The ordinary spore print color in the species of *Phaeomarasmius* is between « burnt umber » and « Alamo », or from « Arab » to « Cognac » (Maerz & Paul). However, the author has observed a species, rather common on various débris on road sides in the mountains of Virginia in cool summers and after heavy rains which though showing all the characters of typical *Phaeomarasmii*, had very light colored spores. The spore print was a light ocher yellow (« Nankeen » of Maerz & Paul), and the spores under the microscope were from nearly hyaline to stramineous. This species is undescribed (*P. gregarius* ad int.). It is roughly comparable to the genus *Leucocortinarius* as opposed to *Cortinarius*, and the *Tricholoma cystidiosum* of A. H. Smith which in the author's opinion is a pale spored *Inocybe*. Just as *Leucocortinarius* has for a long time been considered as belonging to *Armillaria*, *Cortinellus*, or *Tricholoma*, so, this Virginian *Phaeomarasmius* might easily be confused with *Cystoderma* if mistaken for a leucosporous form. However, it must be kept in mind that the number, shape and size of the cheilocystidia is very different from that of the Cystodermas, and the habit, appearance and affinities of this form are all with *Phaeomarasmius* rather than with *Cystoderma*, even if it would be admitted that there are species with ochraceous spore print in the latter genus which at present cannot yet been considered as established beyond a doubt.

State of knowledge : Some of the species of *Phaeomarasmius* are rather well known. They have been studied by the author, and are considered as undoubtedly belonging in the genus *Phaeomarasmius,* and as different from each other. Sixteen species of this category are known at present, and enumerated below. But further investigations are bound to show a larger number of species as belonging to this genus.

Practical importance : Some species, especially the typical lignicolous species, may contribute to the death of diseased trees. Since they often occur on fruit trees, this means that their practical importance in plant pathology is probably underestimated at present.

SPECIES

Subgenus I. **Rimulincola** Sing (1948) Non incrusted spherocysts absent or rare.

Type species : P. horizontalis (Bull. ex Fr.) Kühner.

P. confragosus (Fr.) Sing. (Pholiota, Karst ; Fulvidula, Sing. 1937 ; Naucoria, Sing. 1948) ; *P. rufolateritius* (Bres.) Sing. (Crepidotus, Bres.) ; *P. aridus* (Pers.) Sing. [Agaricus, Pers.; Naucoria erinacea (Fr.) Gillet; Phaeomarasmius, Sing.] ; *P. horizontalis* (Bull. ex Fr.) Kühner [Naucoria, Quél. ; Galera, Quél. ; Naucoria rimulincola (Rab.) Sacc. ; Phaeomarasmius excentricus Scherffel]; *P. distans* (Peck) Sing. (Crepidotus, Peck) ; *P. erinaceella* (Peck) Sing. (Agaricus, Peck ; Pholiota, Peck 1908 ; Agaricus detersibilis Peck non Berk. & Curt.) ; *P. alnicola* (Murr.) Sing (Crinipellis, Murr. ; Naucoria, Sing.) ; *P. gracilis* (Quél.) Sing. (Pholiota muricata var. gracilis Quél.) ; *P. siparius* (Fr.) Sing. (Naucoria, Gillet) ; *P. granulosus* (Lange) Sing. (Naucoria, Lange) ; *P. curcuma* (Berk. & Curt.) Sing. (Naucoria, Sacc.) ; *P. Wieslandri* (Fr.) Sing (Naucoria, Karst) ; also two undescribed species : *P. gregarius* Sing. ined. (Virginia, U. S. A.) ; *P. Malcuccarum* Sing. ined. (Argentina).

Subgenus II. **Carpophilus** Sing. (1948). Non incrusted spherocysts numerous.

Type species : P. carpophilus (Fr.) Sing.

P. carpophilus (Fr.) Sing. (Naucoria, Quél. ; Tubaria, Kühner) ; *P. pygmaeus* (Bull. ex Fr.) Sing. sensu Romagnesi (Naucoria Gillet).

KEY TO THE SPECIES

A. Pileus hygrophanous or non hygrophanous; cells of the epithelium incrusted, or epithelium none. On wood, or on small sticks, rarely on herbaceous debris; lamellae often broadly adnate.

B. American species (for a large, strongly annulate and hygrophanous species see « L »).

C. Elements of the epicutis with a subreticulate crystalline incrustation; stipe somewhat eccentric; margin sulcate when drying. *P. distans*

C. Not incrusted with crystals but rather with resinous matter or pigment.

D. Pileus pilose, terminal members of the epicuticular hairs conical but with rounded tip, 40-100 × 7-8 μ; spores 7.7-9.5 × 5.5-7.5 μ. On *Alnus*. Northwestern North America. *P. alnicola*

D. Not combining these characters. Not known as growing on *Alnus*. Eastern United States and Middle West, South America.

E. Spores 6.3-10 × 4.2-6.2 μ.

F. Epicuticular layer with numerous spherocysts.

F_1 Pileus non-hygrophanous, or nearly so; spore print rusty. *P. curcuma*

F_1 Pileus distinctly hygrophanous; spore print « Nankeen ». *P. gregarius* ined.

F. Spherocysts none.

F_2 Pileus non-hygrophanous, or nearly so. North America. *P. erinaceella*

F_2 Pileus hygrophanous. South America. *P. Malvacearum* ined.

E. Spores larger. On *Crataegus*. Missouri. *P. rufolatericius*

B. European species and species of Northern and Central Asia, Caucasus and North Africa.

G. On cortex; margin sulcate; spores very large (13-16 × 7-9 μ). *P. horizontalis*

G. On sticks, stumps, etc.; spores smaller.

H. Members of the chains of epicuticular elements short, many of them spherocysts.

I. Spores larger than 7.2 μ. *P. granulosus*

I. Spores smaller than 7.2 μ. *P. gracilis*

H. Members of the chains of epicuticular elements elongate and even the majority of the terminal members less than half as broad as long.

J. Few spores more than 10 μ long.

K. Cheilocystidia broader than 10 μ. *P. Wieslandri*

K. Cheilocystidia mostly narrower than 10 μ.

L. Pileus 26-50 mm broad; annulus broad, striate. *P. confragosus*

L. Pileus smaller; annulus indistinct. *P. sparius*

J. Many spores more than 10 μ long. *P. aridus*

A. Pileus more or less hygrophanous; cells of the epithelium not incrusted by pigment On foliage and grasses, herbaceous stems, and on the earth and humus, more rarely on small sticks; lamellae usually narrowly adnexed.

M Pileus punctate with small russet granulations; stipe veiled, apex of the cheilocystidia narrow (as in *Alnicola* sect *Melinoideae*). *P. carpophilus*

M Not combining these characters *P pygmaeus*

GENERA INCOMPLETELY KNOWN, AND GENERA INCERTAE SEDIS

Hebelomina R. Maire, *Bull. Soc. Hist. Nat Afr. N.* **26**: 14. 1935. «Habit tricholomatoid; spores hyaline, amygdaliform as in *Hebeloma*, with rather thick walls; edge of the lamellae heteromorphous because of filamentous, subclavate, flexuous cheilocystidia [hairs] ». R. Maire. The type species is *H. Domardiana* R. Maire from North Africa (December, near Alma, under *Quercus suber*). This species is described as having the spore print « white in thin layer », the pileus viscid, the cuticle consisting of filamentous hyphae, the spores smooth and 11 15 × 4 µ and when young becoming purplish violet with iodine, when mature unchanging.

The position of this genus is completely unknown, even though the description is apparently complete. R. Maire seemed to think that this is close to *Hebeloma*; Singer (1636) put it tentatively in the *Tricholomataceae*. It is not quite clear just how white the spore print is when seen in thin layer, and whether it is still white when seen in thick layer. It also appears puzzling that the spores should react with the Melzer reagent distinctly when young, and not at all when adult.

The author has repeatedly observed a species, smaller than *Hebelomina Domardiana* and with much smaller spores, the wall of the spores comparatively thin for a cortinariaceous species but with endo- and episporium, the episporium very pale yellowish brownish colored, and the lamellae more broadly adnate. Otherwise, this species is very closely related to the *Hebelomina*, showing all the characters of the epicutis, the shape of the spores, the cheilocystidia, the clamp connections, and the habitat on the soil. This species may be very close to *Hebeloma* and congeneric with *Hebelomina* if further observations on the latter should indicate a true affinity with the *Cortinariaceae* rather than with the *Tricholomataceae*. If it is a species of the *Tricholomataceae*, it is certainly unusual because of the thick-walled spores, their shape and their reaction with the Melzer.

It would be interesting to find out whether the spores are uninucleate or binucleate. R. Maire says that the spores are «binucleatae» but whether he refers to the nuclei in the cytological sense is very doubtful, and the figures do not seem to suggest it (see pl. I, fig. 8).

This same question is left unanswered in an interesting, very recent contribution to the *Hebelomina* problem by H. C. S. Huijsman who published a new *Hebelomina* from Holland, *H. microspora* Huijsman, *Rev. Mycol.* 11: 31-33. 1946 [1947]. According to that author, the spores are violet brown in the Melzer reagent and the endosporium is strongly metachromatic in cresyl blue. This would suggest that the spores are pseudoamyloid rather than amyloid, and have a double wall of the type often observed in the *Agaricaceae*. If this means that *Hebelomina* is a genus of the latter family, it would certainly be interesting to find out more about the exact color of the spores in a good print.

At present, it is impossible to tell whether *Hebelomina* belongs to the *Cortinariaceae, Tricholomataceae,* or *Agaricaceae.* Cytological and development studies as well as additional observations on the living carphopores will eventually elucidate this problem.

Quercella Vel., *Ceské Houby,* p. 495. 1921. « Small fungi, with the habit of *Galera*; pileus strongly viscid, hygrophanous, with transparent lamellae; stipe thin, fibrillose, watery fleshy, without belt and without cortina; lamellae free, rather thick, the old ones pale ferruginous; spores almond shaped, smooth. » Velenovsky. The type species of this genus is *Q. aurantiaca* Vél. Neither the generic description nor the description of the type species make it fully clear what fungus this is. One may be impressed by the slimy pileus and the habit, the almond-shaped spores and some other characters that tend to suggest *Phaeocollybia.* On the other hand, it should not be forgotten that Velenovsky's species has no cystidia and smooth spores. It is not merely a question as to whether Velenovsky has looked for cheilocystidia, or not. He must have done so, because he himself states that *Naucoria Christinae, N. hilaris,* and *N. sideroides* differ from *Quercella* because of the presence of cystidia; and these are species of *Phaeocollybia* with *Phaeocollybia* cheilocystidia. Under these circumstances, it would be unwise to make any arrangement for *Quercella* unless specimens have been studied, if they do exist. It seems improbable that there is a truly unknown genus in Europe, i. e. a genus based on a species that has never been observed by anybody but Velenovsky.

Ryssospora Fayod, *Ann. Sc. Nat., Bot.* VII. 9: 361. 1889. « Differs from *Pholiota* by the mucilaginous, little developed cuticle, the corticated stipe, the elongate, ventricose stipe, and especially the ferruginous, wrinkled punctate spores with thin endosporium, without germ pore. This genus seems to be close to the higher *Flammopsis* [part of *Pholiota*] from which it does not differ except by the veil ». Fayod. This description is very ambiguous and incomprehensible. It is not clear what Fayod had studied when he published this genus. It is also not clear which species he would have preferred as the type species. Singer & Smith in their recent proposals (*Mycologia* 38: 284. 1946) assumed that it might have been *Flammula apicrea* (Fr.) Gillet. This species does not appear to be accepted by all authors in the same sense, but Bulliard's plate, cited by Fries, certainly represents either a *Gymnopilus* or a *Pholiota* (formerly *Flammula*). Both these genera have priority over *Ryssospora*. Konrad & Maublanc think that *Flammula apicrea* is merely a mild form of *Pholiota alnicola*. If this is true, it is evident that Fayod did not intend to include it in his genus since he described the spores as rough and those of *P. alnicola* are smooth. As for another species indicated by Fayod, «*Flammula marginata*» — it does not exist, and if it is assumed that Fayod meant *Pholiota marginata*, now usually called *Galerina marginata*, it is certainly not correctly described in the generic diagnosis given for *Ryssospora*. *Pholiota mustelina* was not well known to Fayod himself since he added « (cuticule nulle ?) ». The last species indicated by Fayod, *Naucoria hilaris*, does not fit the generic description either since it has no veil at all. Under these circumstances we have to return to *Flammula apicrea* which must evidently be understood in the sense of Bresadola in order to coincide with Fayod's interpretation, and this would make it a *Gymnopilus*, if Bresadola's illustration and description mean anything. This is therefore assumed to be the correct procedure in the selection of the lectotype, and consequently, *Ryssospora* is indicated as a synonym under *Gymnopilus* but with a question mark since the species on which it is based is not yet fully known.

Locellina Gillet, *Champignons*, p. 428. 1876. « Ochrosporous. A volva tearing at the top, with persistent base, bulbiform; annulus arachnoid; spores brownish. » Gillet. The type species is *L. Alexandri* Gillet from France. It is viscid on the pileus, with a rusty

exaggeration is taken for granted, and if the spores are not smooth as they are shown on Gillet's plate, this might well be a *Cortinarius*. This is what Quelét thinks (*Enchiridion*, p. 78. 1886) who identifies it with *Cortinarius delibutus*. Fayod considers it as one of the genera of his tribus *Cortinariés* which consists of various elements of the genus now recognized as *Cortinarius*. In the author's opinion, it is theoretically impossible to prove that *Locellina* is nothing but *Cortinarius*, but Gillet's picture strongly suggests that genus, and there is scarcely a chance that Gillet's genus belongs anywhere else. Under no circumstances should extra European species be described in or transferred to *Locellina* since they are likely to be something entirely different (e. gr. *L. californica* Earle).

Cyphellopus Fayod, *Ann. Sc. Nat., Bot.* VII, **9**, 365. 1889 [*Acetabularia* (Berk.) Sacc., *Syll.* **5**: 6. 1887, non Lamour.; *Agaricus* subgen. *Acetabularia*, Berk., *Linn. Soc. Journ.* **18**: 389. 1881]. « Velum universaliter a pileo discretum; hymenophorum discretum; lamellae liberae; sporae pallide fulvae v. brunneae. » Berkeley. This diagnosis is emended and translated by Massee, *British Fungus Flora* **2**: 232. 1893 as follows: « Pileus regular; gills free from the stem; stem central; universal veil present, remaining as a volva at the base of the stem; spores tawny or brown ». The type species is *Agaricus acetabulosus* Sowerby ex Berk., Sowerby pl. 303. As for the plate, some may be inclined to see in it a *Pluteus*, some a *Coprinus*. Berkeley said that the original specimen was (1881) still attached to the original plate. In this case it should be an easy task for any modern taxonomist to tell where this species belongs. Sowerby makes the following comment on his species: « Found near Millbank, Westminster [England]... This is very like a poor specimen of *Agaricus congregatus* [*Coprinus micaceus*] but the pileus is more plaited. The lamellae are remarkably glandular on their sides; and instead of a bare base it stands in a little socket like volva. » Massee (l. c., p. 233) says: « The present species has not been noted since Sowerby's time, and is a very uncertain production. Judging from the magnified section of the gills [in Sow. pl. 303], the glands on their sides are cystidia. » Saccardo recognized Berkeley's subgenus as a genus but later put it in synonymy with *Locellina* Gillet. The same procedure is also followed by Cooke. This is undoubtedly a mistake. Already W. G. Smith, Massee, and Fayod pointed out that *Locellina* is not generically identical with *Acetabularia*. Yet, *Acetabularia* is a homonym of an older algal genus. Therefore, Fayod's proposal of

a new name for *Acetabularia* (Berk.) Sacc. is nomenclatorially correct and acceptable. Fayod has not seen the species himself but thinks, evidently judging from what is known from publications in the English literature, that *Cyphellopus* (= *Acetabularia*) is comparable to *Volvariella* and close to his own section *Celluloderma* of *Pluteus*. If so, it might be identical with *Pluteus semibulbosus*. For more guesses as to its identity, see Pearson, *Trans. Brit. Mycol. Soc.* **20**: 54-55. 1935 (Annotations by Quélet, René Maire, and Rea).

Whatever the final result — *Cyphellopus* has no chance of being a valid genus under the present arrangement.

Nemecomyces Pilát, *Ann. Mycol.* **31**: 54. 1933. « Carphopores hard, leathery fleshy, little shrinking on drying and bone hard; with universal veil which leaves verrucose scales on the pileus, fimbriate bodies on the margin, and a scarcely distinct volva which is appressed to the stipe; partial veil absent; lamellae adnexed, not decurrent; spores smooth, argillaceous; basidia 4-spored; cystidia none » Pilát. The type species was collected in the Mongolian Peoples Republic, near Kobdo, by Baranow, and communicated to Pilát by Murashkinsky. It was named *Nemecomyces mongolicus* Pilát.

The author has seen nothing quite similar to this in his travels in Central Asia. Imai thinks that this is probably identical with *Tricholoma mongolicum*. If this is so — *T. mongolicum* is indeed common in Mongolia — one must assume that most data given by Pilát are erroneous.

Weinzettlia Vel., *České Houby* **3**: 514. 1921. « Fleshy fungus with the appearance of *Cortinarius cinnabarinus*; pileus convex, innately scaly; stipe cylindrical... brittle fleshy, fibrillose outside, canaliculate hollow from the start...; lamellae distant, thick; stipe in the young stage connected with the pileus by a fibrillose cortina; spores ovoid, smooth, yellow; cystidia on the edge and on the sides of the lamellae, pillar shaped, rounded; spore print rusty. » Velenovsky. The type species is *W. rubescens* Vel. from Czechoslovakia, with red viscid pileus and white, red fibrillose stipe, flesh and lamellae reddening on injury; spores 8-10 µ long, growing on black humus. The author has not seen specimens. This may be anything from a truly new genus to a species of *Cortinarius* (with subsmooth spores), *Inocybe*, *Pholiota*, etc. Without critical type studies, or studies on topotypical specimens, more comment is senseless.

Ramicola Vel., *Mykologia* **6**: 76. 1929. « By its affinity approaching

eccentricity, and the color of the spore print, lack of a veil, solid stipe from the former, and by the involute margin, the eccentric pileus, the spore shape and color, and the solid stipe from the latter. By its habit, it fully reminds one of *Pluteus* but this has different spore color and different cystidia. The spore color seems to be similar to that of the genus *Psilocybe.*» Velenovsky. The type species is *R. oleracea* Vel. from Czechoslovakia. From the diagnosis one would guess that this is identical with *Melanotus* Pat., but the description of the type species is reminiscent of certain species of *Naucoria*, e. gr. *centunculus*. The genus is hardly autonomous, but it is impossible to state with which genus it is identical unless type specimens are available for reexamination.

CREPIDOTACEAE (Imai) Sing.

Type genus : Crepidotus (Fr.) Quél.

Syn. : Crepidoteae Imai, *Journ. Fac. Agr. Hokk. Imp. Univ.* 43 : 238. 1938

Characters : Spore print brownish to light brownish yellow and spores neither provided with a germ pore nor with exosporial ornamentation in the form of warts, without a plage, without a strongly developed differentiation of endo and episporium, not angular in any view ; if ornamented, the ornamentation is due to imbedded spines which cause the spores to appear punctate when focussed upon their upper surface, or else echinulate but then the spores always very small and globose ; habit omphalioid to collybioid, or pleurotoid to clitocyboid, hyphae with or without clamp connections ; the usual reagents without much action, not causing color reactions with the carpophores ; hymenophoral trama not distinctly bilateral, and if there are conductive elements, these are also not arranged in a bilateral manner ; tissue at times partly gelatinized, nonamyloid ; veil thin membranous to cortinoid, or absent ; lamellae not repeatedly forked ; cheilocystidia often present, but pleurocystidia never observed ; spores uninucleate or binucleate. On various débris, wood, humus, soil, sand, deep moss, etc.

Limits : The *Crepidotaceae* are intermediate between the *Cortinariaceae* and the *Rhodophyllaceae*, and they are also close to the *Paxillaceae*. They differ from the *Cortinariaceae* in the different structure of the spores, and from the *Rhodophyllaceae* in the non angular

spores. *Tubaria* may be considered as coming closest the *Cortinariaceae*, in fact it has been considered as a genus of the latter family until very recently. However, the ornamentation of the species with truly ornamented spores (e. gr. *T. thermophila*), the thin and almost simple, easily collapsing wall of the spores, and a general coincidence of the characters of this genus and *Crepidotus* in most of the essential points, seem to prove that *Tubaria* is much closer to the type genus of the *Crepidotaceae* than it is to the *Cortinariaceae* (*Galerina*, and related genera). The genus *Ripartites* differs from the *Cortinariaceae* by its peculiar spores which are uninucleate according to Kuhner. The genus *Pleurotellus* is undoubtedly the genus closest to *Clitopilus (Rhodophyllaceae)* in spite of the fact that it has, for a long time, been wrongly considered as a genus of the *Tricholomataceae*. It differs from *Clitopilus* in the slightly more yellowish color of the spore print, in the more elongate spores and in the non angular ouline of the spores when they are seen from one end. It thus appears to be removed from the *Rhodophyllaceae* and must be inserted in the neighborhood of the genus *Crepidotus* from which it differs in the combination of several characters, viz. shape and color of the spores, and non-gelatinized, clampless hyphae.

The *Paxillaceae* are also rather closely related to the *Crepidotaceae*. Some authors have insisted in considering *Paxillus panuoides* as a *Crepidotus*, and several species described in *Crepidotus* have turned out to be *Paxillus* and vice versa. The difference between the two genera consists in the structure of the hymenophoral trama and the reactions obtained with the fresh carpophores by using alkalis and iron compounds. The proximity of the *Paxillaceae* is rather an indirect one, considering that they are very close to the *Cortinariaceae* and to *Clitopilus (Rhodophyllaceae)*, i. e. a taxonomic constellation like that of the *Crepidotaceae*.

Phylogeny: It is difficult to tell whether the *Crepidotaceae* are closer to the *Paxillaceae*, or to the *Cortinariaceae*. If the latter is true, they may be considered as a — in many regards somewhat primitive — side branch of the latter family, leading, in the end, to the *Rhodophyllaceae*. If the former is true, they must be considered as a ramification of the group that has its origin in the primitive « *Boletineae* », and then the *Rhodophyllaceae* would be an end ramification of the « *Boletineae* ». Since the *Paxillaceae*, parallel to the *Crepidotaceae* taxonomically and in some other regards, are undoubtedly part of the « *Boletineae* » group of families, the author tends to

believe that the *Crepidotaceae* are a similarly derived terminal or intermediate ramification of the «*Boletineae*» system. The author puts the word «*Boletineae*» in quotation marks because it is not used as a taxonomic term in the present work — mainly because of the difficulties of delimitation of a suborder of this kind — but the term is historically well founded and clear enough to characterize a group of families, reaching from the *Strobilomycetaceae* and *Gomphidiaceae* to the *Boletaceae* and *Paxillaceae*, or even further.

Within the family *Crepidotaceae*, *Ripartites* and *Tubaria* appear to be early starting points from which the author tentatively derives *Crepidotus*, and from *Crepidotus* — *Pleurotellus*, the latter genus leading to the *Rhodophyllaceae*.

KEY TO THE GENERA

A. Habit of the carpophores clitocyboid, collybioid, or omphalioid

B. Spores not small and globose, not echinulate but either smooth (or walls slightly crumpled-rough) or with imbedded short spines, binucleate (according to Kühner); habit collybioid to omphalioid. 131. *Tubaria*

B. Spores small (5 µ or less), echinulate, uninucleate (according to Kühner); habit clitocyboid. 132. *Ripartites*

A. Habit of the carpophores pleurotoid.

C. Spores under the microscope melleous to brownish melleous or pale rusty melleous, never oblong or cylindric and at the same time smooth; clamp connections either present or absent; spore print «clay color», «honey yellow» (R.), «oak wood», «terrapin», pl. 13, K 10 (M. & P.) 133. *Crepidotus*

C. Spores under the microscope yellowish, and smooth; clamp connections absent; spore print «cream buff», «chamois» (R.) «cork» (M. & P.) 134. *Pleurotellus*

131. TUBARIA (W. G. Smith) Gillet

Champignons, p. 537. 1876. em.

Type species: *T. furfuracea* (Pers. ex Fr.) Gillet.

Syn.: *Agaricus* subgenus *Tubaria* W. G. Smith, *Clavis Agar.* p. 21. 1870.

Characters: Habit omphalioid to collybioid, pileus hygrophanous or non hygrophanous, non-viscid; pileus with a cuticle consisting of repent or at least not erect hyphal elements, some of them in some species strongly incrusted by an intercellular or epicellular pigment, some of the hyphae with guttulate contents in some species, without any dermatocystidia or sphaerocysts, and not forming a trichoder-

mium or palisade; lamellae adnexed to decurrent, rather narrow to more often broad; hymenophoral trama regular to subregular; spores with non ornamented wall which is indistinctly double or simple, or with an ornamentation of type XI (very short, imbedded spines in the outer portion of the spore wall), the smooth spores easily collapsing after reaching maturity (and the wall often crumpled rough for that reason), reniform to almond shaped, or ellipsoid to almost boat-shaped or subcylindric, without germ pore or callus, without plage, rather small (but more than 5 μ long) to medium sized (somewhat above 10 μ), brownish (ochraceous cinnamon, light ferruginous ochraceous, etc.) in various (not very deep) shades, e. gr. « Gold leaf » « Mosul » (Maerz & Paul) when observed in print; basidia normal but sometimes 2 spored; cystidia none on the sides of the lamellae but the edge of the lamellae always heteromorphous or nearly heteromorphous from the cheilocystidia which are of varying shape and size according to the species, and often even in a single preparation but always conspicuous, rarely with finger-like appendanges; stipe central and as long or more often longer than the diameter of the pileus, with or without veil, more frequently with a thin membranous white or whitish veil that only very rarely leaves an annular belt, without pseudorrhiza; hyphae of the context with clamp connections. On various dead vegetable matter, fallen fruits, leaves, needles, on wood, deep moss, and on the soil or sand.

Development of the carpophores: Hemiangiocarpous in *T. furfuracea* according to Walker, and probably hemiangiocarpous in all species of *Eu Tubaria*; unknown in sect. *Thermophila.*

Area: Probably cosmopolitan.

Limits: This genus differs from all other genera of the *Crepidotaceae* by the characters of the spores, combined with the characters of the carpophore (central stipe) and seems to be closest to *Crepidotus*. The section *Eu Tubaria* corresponds to the section *Laevisporae* of *Crepidotus*, and the section *Thermophila* corresponds to the section *Echinosporae* of *Crepidotus.*

Tubaria is separated from *Galerina* by several important characters, in the first place by the characters of the spores which have thinner walls with a simpler structure, no plage and no verruculose ornamentation; the section *Tubarioides* of *Galerina*, without plage, differs in having clampless septa. The genus *Phaeomarasmius* differs in the structure of the epicutis (among other characters of equal weight), and the Naucorias differ in the same character. Their spores

may appear somewhat similar under the microscope, due to the fact that they are also rather thin walled in *Naucoria* and *Phaeomarasmius* but the differentiation of the endosporium is usually more readily discernible in these genera than in *Tubaria*. One species of *Phaeomarasmius* has been inserted in *Tubaria* by several authors, mainly by Kühner. But this species has a very different structure of the covering layers of the pileus and the stipe, and is actually close to the other *Phaeomarasmii* rather than to *Tubaria*.

A few species of *Tubaria* in the wider sense (such as it was originally interpreted by Fries and Saccardo) have nothing in common with either *Tubaria* sensu Romagnesi, Singer, or the *Cortinariaceae* in general. They belong in *Deconica*, and differ from the genera named above in having much deeper colored spored print, and spores with a very conspicuous germ pore.

State of knowledge : Romagnesi was the first and only author who has paid attention to the taxonomy of this difficult and generally neglected genus. The species that were treated by him, are European species, and his keys do not seem to cover the American material. The European species are restricted to a single section. The author admits at present all the species admitted by Romagnesi, and in addition some American species. This brings the number of known Tubarias up to 11. However, it would be desirable to have a monograph based on material from all over the world since it is at present impossible to determine any non European material (except for a few American species, with even a modest degree of assurance.

Practical importance : None.

SPECIES

Sect. 1. **EU-TUBARIA** Sing. (1948) Spores without imbedded ornamentations, more or less smooth, at least when quite fresh ; pileus more or less hygrophanous ; veil slightly to strongly developed.

Type species : *T. furfuracea* (Pers. ex Fr.) Gillet.

European species (possibly also occurring in America):

T. autochthona (Berk. & Br.) Sacc. ; *T. minutalis* Romagnesi ; *T. pallidospora* Lange ; *T. pseudoconspersa* Romagnesi ; *T. conspersa* (Pers. ex Fr.) Fayod sensu Romagnesi (Naucoria, Quel.) ; *T. trigonophylla* (Lasch) Fayod sensu Cooke (T. furfuracea ssp trigonophylla Sacc.) ; *T. furfuracea* (Pers. ex Fr.) Gillet ; *T. pellucida* (Bull. ex Fr.) Gillet sensu Romagnesi.

American species (possibly also occurring in Europe):

T. subcrenulata Murr.; *T. fuscifolia* Murr.

Sect. 2 **THERMOPHILA** Sing. (1948) Spores with imbedded short spines, punctate when seen from above; pileus not or not distinctly hygrophanous; veil none.

T. thermophila Sing.: also an *Omphalina* like species from Argentina.

KEY TO THE GENERA

For the species of Europe, see Romagnesi in *Rev. Mycol.* **8**: 34-35. 1943.

132. RIPARTITES Karst.

Hattsv., Bidr. Finl. Nat. Folk **32**: xxiv. 1879.

Type species: R. tricholoma (A. & S. ex Fr.) Karst.

Characters: Pileus whitish to rusty brown or argillaceous brown, often with appressed fibrillose squamules or with fimbriate margin, slightly to strongly sticky-viscid, depressed in age, with involute margin, sub-hygrophanous or non-hygrophanous; cuticle not organized into a trichodermium or a hymeniform structure, without dermatocystidia and without spherocysts; lamellae decurrent or adnate; hymenophoral trama rather regular, consisting of somewhat interwoven hyphae but generally axillarly arranged, the hyphae filamentous; basidia very small, normal; cystidia none on the sides of the lamellae, but cheilocystidia somewhat differentiated; spores in print between « Desert » and « Bamboo » (Maerz & Paul), under the microscope pale brown, echinulate, very small and globose, generally reminding one of the conidia of some *Aspergillaceae* but asymmetric (heterotropic); nonamyloid, without germ pore and callus, with apparently simple wall, uninucleate according to Kühner; stipe central or nearly so, well developed; veil present, cortinoid or thinly membranous, soon disappearing without leaving very distinct marks on the mature carpophores; all hyphae with clamp connections, nonamyloid. On rotten débris in the forest, also on humus and sand and among mosses.

Development of the carpophores: Unknown.

Area: Temperate zones of the Northern Hemisphere; Argentina.

Limits: This genus is well separated from all other genera of the *Agaricales*. It often resembles a *Clitocybe* but the colored spores and the veil will immediately give it away. Among the *Crepidotaceae*, it

seems to be most closely related to *Crepidotus* which differs in larger spores and pleurotoid habit. Larger specimens of *Crepidotus* with well developed and occasionally subcentral stipe can still be separated by the size of the spores and the character of their ornamentation. *Ripartitella* can easily be mistaken for *Ripartites* but the hyaline spores, dry pileus, and the peculiar cystidia separate it from *Ripartites*.

State of knowledge: Four species of *Ripartites* are known completely. Only one species has been studied cytologically, and the individual development of the carpophores has been neglected entirely.

Practical importance: None.

SPECIES

R. strigiceps (Fr.) Karst. (Flammula, Quél.); *R. tricholoma* (A. & S. ex Fr.) Karst. (Flammula, Quél.; Inocybe, Kalchbr.; Paxillus, Quél. 1886; Astrosporina, Schröter; Paxillopsis, Lange); *R. helomorphus* (Fr.) Karst. (Flammula, Quél.); *R. Amparae* Sing.

KEY TO THE SPECIES

A. Pileus with erect or semierect small ciliate hairs, these hairs larger and more squamulose near the center, more ciliate and pallid near the margin. *R. strigiceps*

A. Pileus with hairs only on the margin, or without any hairs

  B. Pileus convex and depressed or umbilicate at the center; margin strigose-ciliate. *R. tricholoma*

  B. Pileus somewhat umbonate in the center.

    C. Margin glabrous. *R. helomorphus*

    C. Margin squarrose-fibrillose. *R. Amparae*

133. CREPIDOTUS (Fr.) Quél.

Champ. Jura Vosges, p. 138. 1872-73

Type species: C. mollis (Schaeff. ex Fr.) Quél.

Syn: *Agaricus* tribus *Crepidotus*, *Fr. Syst. Mycol.* 1: 272. 1821
Dochmiopus Pat., *Hymen. Eur.* p. 113. 1887.
Derminus Schröter in Cohn, *Krypt.-Fl. Schlesien, Pilze* 1: 578. 1889.
Tremellopsis Pat. apud Duss, *Fl. Crypt. Ant. Fr.*, p. 223. 1904
Conchomyces Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 19. 1927.
? *Phialocybe* Karst., *Bidr. Finl. Nat. Folk* 32: xxii. 1879

Characters : Habit pleurotoid; pileus with an indefinite cuticle, or if the cuticle is well differentiated, the latter consists of repent or ascendant to erect, thin, filamentous hyphae which sometimes are forked, rarely with very scattered and inconstant dermatocystidioid bodies, the colored species having the walls of the superficial hyphae incrusted by an epimembranal or a membrana pigment, but more species are between rusty or brown and white, more often closer to the latter, i. e. hyphae all devoid of pigment; underneath the cuticle or the surface layer, in many species, a narrower to broader layer of strongly gelatinized hyphae (Pl. XX, 4); lamellae variously attached to the base, or concurrent, rounded or attenuate, often decurrent if a stipe is present, not connected by anastomoses, narrow or broad; hymenophoral trama regular to subregular, consisting of interwoven to subparallel hyphae, at times all of them running in different directions and — though they are all elongate to filiform — rather versiform in a single preparation but always the majority strictly axillarly arranged, usually pigmentless but in a few species slightly pigmented, in one species with crystalline vinaceous pigment, the hyphae varying in density, from loosely arranged to rather densely packed; spore print about «clay color» (Ridgway), in some species more yellowish than «clay color» (reaching «honey yellow» in others more cinnamon, viz between «oak wood» and «Terrapin» (Maerz & Paul), or pl. 13, K 10 but never as deep fuscous or rusty as in the *Strophariaceae* (*Melanotus* and *Pleuroflammula*), melleous to brownish melleous, often rather pale and with a rusty tinge (from the imbedded ornamentations, under the microscope, with rather thin and simple wall, but in some species with an indistinct endosporium, the outer stratum of the wall often perforated with imbedded, very short cylindric spines which are usually somewhat deeper colored than the episporium, and make the spores appear punctate when the upper surface is focussed upon, or else entirely non ornamented, from nearly perfectly globose (but with oblique hilar appendage) to rather oblong in certain species (but then never smooth), often ellipsoid or short-ellipsoid, and at times with mucronate apex, without a germ pore, but occasionally with an indistinct callus; basidia normal; cystidia none on the sides of the lamellae but always present on the edges (cheilocystidia); the latter are not always crowded enough to make the edge heteromorphous but usually rather numerous, varying in size and shape according to the species and often rather versiform in

paratively short and more or less eccentric, sometimes rudimentary, visible only from below (hymenophoral surface), not from above, or else well developed in the primordia and then gradually oblitterated; veil none, or very indistinct; context consisting of hyphae, with or without clamp connections. On wood, and herbaceous stems, rarely on the earth, or on fallen parts of ferns, palms, etc. Chemical reactions with the ordinary reagents rather weak.

Development of the carpophores: Unknown.

Area: Cosmopolitan.

Limits: This genus can be separated from all genera of the *Crepidotaceae* according to the characters indicated in the key. The genus most closely related to it, is *Pleurotellus* which can be distinguished by several correlated characters.

In other families, there are certain species which have been confused with the *Crepidoti* but actually are not very closely related though, at times, they may look somewhat similar. These are *Pleuroflammula, Melanotus,* and *Pyrrhoglossum.* The latter has more richly colored, warty spores and darkens with alkalis; *Pleuroflammula* and *Melanotus* have a different type of spores, especially the latter genus where the spores are strikingly truncate from a well developed germ pore.

Some authors consider *Paxillus panuoides* as a *Crepidotus,* but the differences between that species and all the other *Crepidoti* are so striking, and the similarities between it and the other *Paxilli* so numerous, it can scarcely be expected to be retained in *Crepidotus* in a modern classification.

State of knowledge: This genus was neglected in Europe until Josserand's study of *C. applanatus* and *C. fragilis,* Favre's study of the species of *Dochmiopus* Pat. (a synonym of *Crepidotus*), and the author's notes on *C. variabilis* (1928) and the other *Dochmiopus* (1936) appeared. Even so, the determination of the species of *Crepidotus* in Europe was still very difficult. In *North American Flora,* Murrill gave an uncritical account of all the species described, but many of these were synonyms, or did not belong to *Crepidotus* proper, and those that remain are keyed out not according to their important characters. The author has recently started monographic work on the world flora of *Crepidotus,* and the first results were published in *Lilloa* 13: 59-95. 1947. On the basis of this latter paper, 36 species are now recognized which are enumerated below.

Practical importance: Some *Crepidoti* are rather harmless wood-

destroyers (e. gr. *C. paxilloides* on oak ties) Other species are edible. In Java, two species are eaten, *C. verrucisporus* (Van Overeem) Sing. («soepa amis») and *C. edulis* Van Overeem («soepa djengkol»).

SPECIES

Sect. 1. **ECHINOSPORAE** Pilát (1929). Spores with heterogeneous wall, punctate when the upper surface is focussed upon because of very short, cylindric, imbedded spines which are usually of slightly deeper color than the remaining part of the spore wall.

Type species : *C. carpaticus* Pilát.

Subsection **Porpophorini** Sing. (1947). Hyphae with numerous clamp connections.

Type species : *C. applanatus* (Pers. ex Fr.) Quél.

Stirps **Roseus** (Hyphae of the hymenophoral trama with bright colored crystallized pigment).

C. roseus Sing.

Stirps **Nyssicola** (Pigment not bright; stipe comparatively well developed, not concrescent with margin; pileus and cheilocystidia large).

C. nyssicola (Murr. ex) Sing.

Stirps **Applanatus** (Pigment not bright; stipe poorly developed or none in adult specimens, spores more or less globose).

C. applanatus (Pers. ex Fr.) Quel. sensu Josserand; *C. fulvifibrillosus* Murr.; *C. crocophyllus* (Berk.) Sacc [C dorsalis (Peck) Sacc.]; *C. cuneifolius* Pat. (C. aquosus Murr.); *C. quitensis* Pat. (C. parvulus Murr.); *C. praelatifolius* Murr.; *C. cinnamomeus* Smith & Sing.; *C. nephrodes* (Berk. & Curt.) Sacc. [C. malachius (Berk. & Curt.) Sacc.; C. malachius var. plicatilis Peck; C. hygrophanus Murr.; apparently also the same or forms of the same species: C. putrigenus (Berk & Curt.) Sacc.; C. palmularis (Berk. & Curt.) Sacc., and C. leteochrysus (Berk. & Curt.) Sacc.]; obviously also *C. verrucisporus* (Van Overeem) Sing. (Conchomyces, Van Overeem).

Stirps **Variabilis** (Pigment not bright; stipe poorly developed or none, or small in adult specimens; spores more than 1 μ longer than broad, often strictly elongate).

C. Eucalypti (Torr.) Sing. (Claudopus, Torr.); *C. croceotinctus* Peck; *C. sphaerosporus* (Pat.) Sing. [Agaricus variabilis var. sphaerosporus Pat.; Agaricus sphaerosporus Pat. apud Roumeguere; Doch

miopus sphaerosporus (Pat.) Pat.; Claudopus, Sacc.]; *C. brunswickianus* (Speg.) Sacc.; *C. Cesatii* (Rab.) Sacc. (Dochmiopus, Konr. & Maubl.); *C. paxilloides* Sing. (Paxillus reniformis Berk. & Rav.; Crepidotus, Sing. non Velenovsky); *C. variabilis* (Pers. ex Fr.) Quél. [Claudopus, Gillet; Dochmiopus, Pat.; C. chimonophilus (Berk. & Br.) Sacc. sensu Sydow]; *C. luteolus* (Lambotte) Sacc. (Dochmiopus, Kühner); *C. submollis* Murr. (C. pubescens Bres.); probably also *C. carpaticus* Pilát. (provided it has clamp connections); also an undescribed species on palms in Argentina (*C. palmarum* Sing. ined.).

Subsection Aporpini Sing. (1947). Hyphae without clamp connections.

Type species : C. cinnabarinus Peck.

Stirps **Versutus** (Pigment not bright, and not abundant).

C. versutus (Peck) Sacc.; *C. sublevisporus* Sing. ined.; *C. defibulatus* Sing. ined.

Stirps **Cinnabarinus** (Pigment bright and abundant).

C. cinnabarinus Peck.

Sect. 2. LAEVISPORAE Pilat (1929). Spore wall homogeneous.

Type species : C. mollis (Bull. ex Fr.) Quel.

Subsection Fibulatini Sing. (1947). Hyphae with numerous clamp connections.

Type species : C. albidus Ell. & Ev.

Stirps **Albidus** (Spores very short).

C. albidus Ell. & Ev.; *C. amarus* Murr.

Stirps **Antillarum** (Spores more or less elongate).

C. Betulae Murr.; *C. fragilis* Josserand (C. autochthonus Lange; *C. Antillarum* (Pat. in Duss) Sing. (Tremellopsis, Pat. apud Duss; C. cinchonensis Murr.); *C. acanthosyrinus* Sing. ined. (Argentina).

Subsection Defibulatini Sing. (1947). Hyphae without clamp connections.

Type species : C. mollis (Bull. ex Fr.) Quél.

C. calolepioides Murr.; *C. calolepis* (Fr.) Karst. (C. fulvotomentosus Peck); *C. alveolus* (Lasch) Karst. sensu Britz.; *C. uber* (Berk. & Curt.) Sacc. (C. sulcatus Murr.; most probably also C. Citri Pat.): *C. mollis* (Bull. ex Fr.) Quel. [C. haerens (Peck) Sacc.; C. alabamensis Murr.; C. fraxinicola Murr.]; *C. variisporus* Sing. ined. (Argentina).

KEY TO THE SPECIES

A. Spores punctate, wall heterogeneous (noticeable only under a good oil immersion lens), with an ornamentation of type XI.

B. Clamp connections present.

C. Tramal hyphae with vinaceous lilac crystallized pigment. Florida. *C. roseus*

C. Tramal hyphae hyaline, or almost so.

D. Stipe strongly developed, eccentric; cheilocystidia very long and rather broad (49-80 × 9-13 μ); pileus 40-50 mm broad; Florida. *C. nyssicola*

D. Stipe usually indistinct when seen from above (i. e. from the side of the carpophore that is opposite the hymenophore), or in smaller forms often present but very small and eccentric and often disappearing in mature specimens; cheilocystidia rarely reaching the size indicated above; pileus rarely larger than 40 mm in diameter.

E. Spores virtually globose, i. e. length less than 1 μ larger than breadth in an average of mature spores, or just 1 μ larger than breadth (in case of doubt, look for large cinnamon colored fungi here, for small pure white fungi rather in the alternative group).

F. Lamellae narrow and close. Species of the temperate zone.

G. Pileus naked. *C. applanatus*

G. Pileus with appressed fibrillose scales formed by strands of parallel hyphae with fulvous incrustations. *C. fulvifibrillosus*

F. Lamellae broad or/and subdistant.

H. Lamellae initially salmon orange; pileus about 20-40 mm broad, comparatively fleshy behind. North America, South America. *C. crocophyllus*

H. Lamellae not initially salmon orange, or else minute fungi, not occurring in North America.

I. Pileus cinnamon buff to watery brown in fresh condition; striate or sulcate, 10-25 mm broad; spores strictly globose or subglobose. Tropical North and Central America. *C. cuneiformis*

I. Pileus some other color, at least when young and fresh and not too watersoaked, often smaller than indicated above, and then spores about 1 μ longer than broad.

J. Spores globose and smaller than 5-7 μ, or rarely a number of macrospores present. South and Central America. *C. quitensis*

J. Spores longer than 5-7 μ

meter) with enormously broad lamellae. Florida. *C. praelatifolius*

K. Carpophores usually much larger, always larger than 8 mm; lamellae not unproportionally broad.

L. Carpophores large and non resupinate, usually sessile-lateral, 30-43 mm broad, occurring in North America; cheilocystidia clavate-capitate.

M. Pileus «vinaceous cinnamon» or some color near this (Ridgway), delicately fibrillose near the margin. *C. cinnamomeus*

M. Pileus white to yellowish, not delicately fibrillose at the margin but often fibrillose-tomentulose all over. *C. nephrodes*

L. Carpophores usually much smaller than indicated above, or else attached with some point of the surface of the pileus rather than with the margin. Uncommon in North America; cheilocystidia clavate-capitate or some other shape (see «N»).

E. Length of the spores more than 1 μ larger than the breadth, at least in a large number of the spores of a print.

N. Spores, at least the broader ones, with very distinct punctation, which is obvious under high dry objective.

O. Spores longer than 7 μ or broader than 4 μ.

P. Dried specimens pure white; spores almost subglobose, 6.8-8.2 × 5.8-6.8 μ. On *Eucalyptus* in the Mediterranean region and on the Azores. *C. Eucalypti*

P. Dried specimens usually not strikingly pure white; spores as indicated above or more elongate; not on *Eucalyptus* in the regions indicated above.

Q. Spores 6.2-7 × 4.8-5.3 μ; pileus «light buff», dorsal portion often «ochraceous tawny» (Ridgway). North America from New York to Florida. *C. croceotinctus*

Q. Spores, at least their majority, longer and usually also broader than indicated

above; pileus not colored as indicated above

R. Carpophores thin, fragile.

S. Pileus villous or tomentose in the dorsal portion in nearly all specimens. On various hosts, fallen parts of trees, shrubs, or herbaceous plants, not, or rarely, on *Platanus*

T_1. Pileus white when fresh, pubescent. Neither on palms nor on subantarctic hosts

C. sphaerosporus

T_2. Pileus pale melleous to fulvous-yellowish, glabrous. On *Nothofagus* and *Maytenus*.

C. brunswickianus.

T_3. Pileus near pl. 12, J-8 (Maerz & Paul). On *Cocos Romanzoffiana*.

C. palmarum ined.

S. Pileus entirely glabrous, even in the dorsal portion, or appearing so in dried specimens; on *Platanus* in the Mediterranean region.

C. Cesatii

R. Carpophores rather thick. On oak rails in North Carolina

C. paxilloides

O. Spores smaller, narrower: 5.5-6.8 × 3.3-3.5 μ.

C. variabilis

N. Spores very indistinctly, faintly, and slightly punctate, punctation just barely visible with the best equipment.

U. Pileus yellow, especially near the dorsal portion but fading in age, not sulcate-plicate. Europe

C. luteolus

U. Pileus white or nearly so, later often discolored, in America often striate to sulcate-plicate. On *Ulmus* in Europe and the American West. *C. submollis*

B. Clamp connections absent.

V. Spore wall very slightly punctate.

Va. Spores 9.8-10.5 × 5.3-6 μ. New York. *C. tersulus*

Va. Spores 5.8-7.4 × 4.8-5.8 μ. Argentina. *C. sublevisporus*

V. Spore wall strongly and distinctly punctate (under an oil immersion)

Vb. Carpophores white (except for the spores). Argentina

C. defibulatus

Vb. Carpophores abundantly pigmented (bright ...

hyphae melleous and incrusted. American Middle West, Europe
C. cinnabarinus

A'. Spores not punctate; wall homogeneous

W. Clamp connections present

X. Spores up to 1 μ longer than broad (subglobose to globose)

Y. Spores 5-6.7 × 4.8-6 μ. American Middle West *C. albidus*

Y'. Spores 6.5-7.3 (8.3) × 5.5-6.3 (6.6) μ. Florida *C. amoenus*

X'. Spores more elongate (short ellipsoid, ellipsoid, apple seed shaped, or subellipsoid with mucronate apex)

Z. Spores up to 8.5 × 5.2 μ; trama of the upper half of the pileus strongly gelatinous; on wood of frondose trees in the temperate zone of North America. *C. Betulae*

Z'. Spores larger than indicated above, or trama little gelatinized. Tropical North America, Central America, South America, Europe, Asia.

AA_1. Pileus with an upper layer of appressed fine fibrils which crack eventually, showing the hygrophanous context; spores 7-9 × 4.8-5.8 μ. Carpophores growing on the earth or on coniferous hosts (very decayed wood) in the temperate regions of the Eastern hemisphere. *C. fragilis*

AA_2. Pileus with a different cuticle; spores somewhat larger (8) 8.2-10.5 (11) × 5.2-6.8 μ. Tropical America, on frondose trunks. *C. Antillarum*

AA_3. Distinctly tomentose (s. l.); spores 6.5-8.5 × 5-6.8 μ. Argentina. *C. acanthosyrinus* ined.

W'. Clamp connections absent

BB. Dorsal part of the pileus beset with spiny small scales. Tropical America *C. calolepoides*

BB'. Scales, if present, always inconspicuous or strictly appressed

CC. Spores (6.8) 7.5-11 × 5.3-7 μ (rarely smaller), only a comparatively thin upper layer of the context of the pileus (up to one third) gelatinous.

DD_1. Pileus naked or almost so; cheilocystidia rather constantly predominantly clavate-elongate. Europe. *C. alveolus*

DD_2. Pileus with ochraceous to rusty, appressed fibrils squamulose; cheilocystidia versiform. Temperate zones of Europe, Asia, and North America *C. calolepis*

DD_3. Pileus without squamulae or with indistinct ones; cheilocystidia, often flexuous, long-filamentous, rarely very slightly subcapitate, with one to three constrictions, often bifurcate at the apex; gelatinized zone of the pileus remarkably narrow (one fourth to one sixth of the diameter of the context); lamellae remarkably linear, 1-2.5 mm broad; spores remarkably variable: (6.8)-7.5-10.5 × (4.8) 6-6.3 μ; South American species of the pre-andine montane zone in wooded ravines on *Cedrela, Celtis, Duranta, Phoebe* or *Prunus*.
C. variisporus

CC. Spores smaller, 7-10 μ long; gelatinous layer occupying at least one half of the trama of the pileus, at least in those species without the subtropical and tropical zones.

EE₁. Subtropical species of South America. Trama of the pileus not gelatinized. (see *C. sublevisporus*)

EE₂. Subtropical montane species of South America. Trama of the pileus gelatinized only one fourth to one sixth of its diameter. (see *C. varitsporus*)

EE₃. Not showing the characters of either « EE₁ », or « EE₂ ».

FF. Lamellae usually rather broad and even ventricose, subdistant to close, the constantly strongly striate to sulcate margin often brown to deep brown, especially in dried specimens; cuticle in microscopical section so thin it usually apears to be almost non differentiated. Subtropics and tropics of North, Central, and South America, Oceania, and Asia. *C. uber*

FF. Lamellae always rather narrow, close to crowded; pileus with subconcolorous to yellowish-olive margin of striate; cuticle well developed, forming a layer of denser hyphae than those of the subjacent layer and the contents of the cuticular hyphae more abundantly protoplasmatic. Temperate species. *C. mollis*

134. PLEUROTELLUS Fayod

Prodrome, Ann. Sc. Nat., Bot. VII. 9 : 339. 1889

Type species: Pleurotus hypnophilus (Berk.) Sacc. sensu Fayod, non. al.

Syn. : *Calathinus* Quel. *Enchiridion* p. 46. 1886, non Rafinesque 18..

Characters: Pileus without a distinct stipe, attached to the substratum by an eccentric or laterally protracted point; cuticle consisting of thin, filamentous, repent, parallel or subparallel hyaline hyphae; lamellae concurrent; hymenophoral trama subregular to intermixed; subhymenium of small, subisodiametric, irregular elements; spore print pale brownish yellow (« cream buff » to « chamois » of Ridgway), or slightly more pinkish (« cork » of Maerz & Paul); spores subhyaline to pale brownish yellow, thin walled, smooth, with entire, homogeneous, nonamyloid wall, not angular in any position; basidia normal; cystidia on the sides of the lamellae none; context very thin; all hyphae without clamp connections. On various dead or living plant material (mosses, grasses, various herbaceous

Development of the carpophores: Unknown.

Area: Europe and North and South America, probably at least all over the temperate zone, and perhaps also in parts of the tropics, but there are not enough records available to substantiate this.

Limits: The genus *Pleurotellus* was originally used in the sense of Quélet's genus *Calathinus* which turned out to be a homonym. This latter genus, in the sense of most authors, is a heterogeneous group of small pleurotoid fungi.

Some of the species were eliminated when the genus *Resupinatus* was defined more clearly (as *Scytinotopsis*, 1936); moreover, the species belonging to *Leptotus* have also been removed. The remaining groups consisted of small species of *Clitopilus*, such as *Pleurotus dictyorhizus* in the sense of most authors, e. gr. Patouillard, *Pleurotus candidissimus*, a rather remarkable and isolated species which is here referred to *Rhodophyllus*, and the group which the author thinks is the original *Pleurotellus* in the sense of Fayod.

Fayod undoubtedly describes the genus correctly, and indicates *P. hypnophilus* as one of its species. This species was chosen as the lectotype of the genus in the sense of Fayod, i. e. not necessarily the original *P. hypnophilus* which nobody seems to know. Fayod has later indicated that he was in doubt himself, whether his *P. hypnophilus* is the true type, since he renamed his species *Pleurotellus graminicola* because it was found on *Poa nemoralis*. However, Peck's *Crepidotus herbarum* has priority, and since there is a good type at Albany, N. Y. it is preferable to use Peck's name rather than any of the Friesian names which are all doubtful. R. Maire calls this species *Crepidotus perpusillus* (Fr.) R. Maire (Agaricus, Fr.; Pleurotus, Gillet; Calathinus, Quél., but the interpretation of *Agaricus perpusillus* of Fries is no less doubtful and uncertain than that of other Friesian names occasionally found on the labels of specimens of *P. herbarum*, such as *Pleurotus septicus* (Fr.) Quél. The interpretation of Fayod's species and genus is very important. There is only one other interpretation possible, and this is the assumption that Fayod had a species of *Clitopilus* (one of the small species which he called *Octojuga*); this, however, is in direct contradiction with the description (« spores légèrement allongées »), and, besides, it would be strange to assume that Fayod who discovered the angular outline of the « *Octojuga* » spores should have overlooked it in the same species, and redescribed it in another genus. Consequently, the only logical and acceptable interpretation of *Pleurotellus* is that expressed in the diagnosis above.

State of knowledge : Only two species are known. These are known in all important details.

Practical importance : *P. chioneus* occurs as a weed fungus in white mushroom beds on the casing, but hardly causes any appreciable damage.

SPECIES

P. herbarum (Peck) Sing. (Crepidotus, Sacc.; Claudopus commixtus Bres.; Pleurotellus graminicola Fayod; Pleurotus hypnophilus sensu Fayod, an Berk. ?); *P. chioneus* (Pers. ex Fr. sensu Pilát) Konr. & Maubl. (Pleurotus, Gillet; Agaricus arenarius Lasch ?, non Lév.).

KEY TO THE SPECIES

As long as only two species are known, these can easily be distinguished by the shape of the spores.

RHODOPHYLLACEAE Sing.

Type genus : *Rhodophyllus* Quél.

Syn : *Rhodogoniosporaceae* Heim, *Treb. Mus. Cienc. Nat. Barcelona* **15** : 86. 1934 (nom. nud.); Sing., *Ann. Mycol.* **34** : 328, 323. 1936 (nom. subnud.). *Jugasporaceae* Sing., *Ann. Mycol.* **34** : 327, 323. 1936 [1].

Characters : Spore print pink (around Pl. XIII, A-7, « French beige », or « woodland rose », « rose beige », « rose beige 2 + », « blush », or Pl. 12, D 8, Maerz & Paul); spores hyaline to substramineous,

[1] This as well as the family name proposed by Heim, and adopted by Romagnesi and the author in his earlier papers, is illegal according to the International Rules of Botanical Nomenclature, Art. 23. The name *Rhodogoniosporaceae* is also illegal because, aside from being formed not from the name of one of the present or former genera of the family, it has never been validly described by any author. Heim did not describe it at all. Singer only keyed it out, and this not in Latin though it was after 1935 and Romagnesi described it later as a series and not as a family. However, the *Jugasporaceae* are validly published (though the name is taken from a tribus rather than a genus of the family) since they were described in French by Kühner before 1935, and the tribus name proposed by Kühner was given a new status by Singer in 1936. This name is now substituted by a nomen novum which is formed according to the rules. *Rhodophyllidaceae* is derived from phyllis, not from phyllos, there can be no question of homonymy, especially since the families belong to different phyla (cf. especially Art. 70, note 4 of the International Rules).

nonamyloid, angular, either in end view (with the longitudinal axis vertical), or in all views, the angles often rather rounded, rarely so rounded, that the spores do not appear angular any more, but then usually at least a few spores mixed in every spore print that show traces of angular outline; habit very different in different species; veil none; hyphae with or more often without clamp connections. On various substrata, often directly on the soil, in the woods as well as outside the woods.

Limits: The family *Rhodogoniosporaceae* was formerly restricted to the genus *Rhodophyllus* and the gastromycetous genus *Richoniella*. The latter genus is here excluded. The author has never studied representatives of that genus, and, in principle, refrains from putting gastromycetous and agaricaceous genera into the same family, at the time being. On the other hand, there are two genera in the agarics which were kept in different families up to very recently but seem to be too close to *Rhodophyllus* to be excluded from the *Rhodophyllaceae*. These genera are *Clitopilus* and *Rhodocybe*.

The latter is often externally so similar to *Lepista* (*Tricholomataceae*) that those species without cystidia were believed to be congeneric with *Lepista nuda* and related Lepistas. The species of *Clitopilus*, on the other hand, were considered by the author as typical for a special small family, the *Jugasporaceae*, which would be one step closer to the *Paxillaceae*, and thus were considered as one of the families of the *Boletineae*.

With the *Clitopili* now recognized as very close to *Rhodocybe*, and these to *Rhodophyllus*, the delimitation of the *Boletineae* becomes obscure since both *Rhodophyllus* and *Clitopilus* are definitely close to *Pleurotellus* which in turn is inseparable from *Crepidotus*. The *Crepidotaceae*, on the other hand, are close to the *Cortinariaceae* because of such genera as *Ripartites* and *Tubaria*. The *Cortinariaceae*, on their part, are inseparable from the *Strophariaceae*. From the point of view of affinities, there is at present no way to delimit the « *Boletineae* », and consequently, there was also no need of retaining the family *Jugasporaceae* (or a substitute name).

With this delimitation, the *Rhodophyllaceae* are distinguishable from the other pink spored genera of agarics:

(1) *Collybia* p. p., *Lepista*, *Macrocystidium* — they all have non angular spores and the hyphae are provided with clamp connections. This combination of characters is scarcely ever found in a species of the *Rhodophyllaceae*.

(2) The genus *Phyllotopsis* differs in non-angular (from all sides), allantoid spores from all pleurotoid species of the *Rhodophyllaceae*; moreover, *Phyllotopsis* is characterized by a hygrophanous tomentum while the pleurotoid *Rhodophyllaceae* are either glabrous or non-hygrophanous.

(3) The genera *Termitomyces* and *Rhodotus* (*Amanitaceae*) differ from the *Rhodophyllaceae* in the distinctly divergent hyphae of the hymenophoral trama, the free lamellae, and the smooth, non-angular spores (in the case of *Termitomyces*), and the finely echinulate, round spores (in the case of the *Rhodotus*)

(4) The genera *Volvariella*, *Chamaeota* and *Pluteus* (*Amanitaceae*) differ in the structure of the trama which is inverse — whereas all the species of the *Rhodophyllaceae* have subregular trama with a slight tendency to bilaterality but with very densely packed hyphae, at least in certain parts of the hymenophoral trama. Besides the lamellae are free in all these genera, the spores non-angular from all sides and in *Volvariella* a volva is present, and in *Chamaeota* an annulus. Both these velar organs are absent in all *Rhodophyllaceae*.

(5) The pink-spored species of the *Agaricaceae* have spores that are punctate, or else smooth, and have a completely non-angular wall which, if homogeneous, is pseudoamyloid.

(6) The « pink- » spored representatives of the genus *Psathyrella* can be distinguished from the *Rhodophyllaceae* by the presence of a germ pore and muricate cystidia.

Phylogeny: It is logical to assume that the genus *Clitopilus* is the most primitive, considering the simpler configuration of the spores, the absence of cystidia, the small number of species, the scarcity of pigment, the ubiquitous habit of most of the species, and the affinity to *Pleurotellus* and, to a lesser degree, *Paxillus*. Compare also comments made under the corresponding heading in the *Crepidotaceae*.

KEY TO THE GENERA

A. Spores not angular in frontal view and in profile, but often rough to warty.
  B. Spores smooth (except for occasional uneven places showing the presence of longitudinal ribs) in profile or frontally. — 135. *Clitopilus*
  B. Spores rough to warty (because of the wavy outline of the wall) when seen in profile or frontally. — 136. *Rhodocybe*

A. Spores angular in frontal view and in profile, never rough and warty, very rarely the majority of spores neither angular nor ornamented (in this case compare genus *Clitopilopsis*, p. 623) — 137. *Rhodophyllus*

135. CLITOPILUS (Fr.) Quél.

Champ. *Jura Vosges*, p. 85. 1872-73.

Type species: *C. prunulus* (Scop. ex Fr.) Quél.

Syn.: *Agaricus* tribus *Mouceron* Fr., *Syst. Mycol.* **1**: 193. 1821.
Agaricus tribus *Clitopilus* Fr., *Epicrisis*, p. 148. 1836; *Monogr.* **1**: 279. 1854.
Hexajuga Fayod, *Ann. Sc. Nat.*, Bot. VII, **9**: 389. 1889.
Octojuga Fayod, *l. c.* p. 390.
Orcella Batt. ex Earle, *Bull. N. Y. Bot. Gard.* **5**: 440. 1909.
Pleuropus Roussel ex Murr., *N. Am. Fl.* **10**: 102. 1917, non (Pers. ex) S. F. Gray (1821).

Characters: Pileus subglabrous to sericeous, smooth or more rarely setose, not viscid or scarcely viscid, small to rather large, the margin initially frequently involute, the color here as in the whole carpophore usually very pallid, i. e. mostly white or whitish, more rarely light gray, or with a creamy ochraceous hue; epicutis consisting of repent, filamentous, hyaline, smooth thin hyphae (Pl. XXVII, 11); spore print pink; hymenophore very rarely poroid rather than lamellate, but normally lamellate in all species; lamellae decurrent (where there is a distinct, persistent stipe); basidia normal, but rarely 1-3-spored, most frequently however 4-spored, and in most individuals at least some basidia 4-spored (Pl. XXVII, 10); cystidia none on the sides of the lamellae, cheilocystidia also scarcely differentiated; however, there is often a large number of abnormal basidia (cystidioles) which do not become individualized enough to be of taxonomic interest; hymenophoral trama consisting of a mediostratum of more or less interwoven, subregularly arranged hyphae, with a generally axillar trend, and a lateral stratum (or more correctly: hymenopodium) which is not sharply differentiated from the mediostratum, differing by the gradually larger volume of hyphae as they approach the subhymenium; hyphae looser in the mediostratum, and more interwoven away from the edge of the lamellae, hyaline; spores (Pl. IX; XXVII, 8-9) hyaline to usually pale stramineous under the microscope, with 5-10 longitudinal ridges, or angles at the borderline between each of the two of the flattened stripes («facettes») running along the sides of the spores, otherwise smooth, without germ pore and without callus, with rather thin and very easily collapsing walls, young spores less distinctly angular, ovoid, ellipsoid-fusoid, always asymmetric (heterotropic); neither amyloid nor pseudoamyloid; stipe

present or absent, if present, often short and inconspicuous or not persistent at maturity; often arising from a mat of mycelium, or a velatinous basal mycelium, without pseudorhiza, without veil; odor often farinaceous; taste mild or bitter; tramal hyphae rather loosely arranged because of a very slight gelatinization of the entire trama as in the boletes; consequently, the context remarkably soft and tender; all hyphae without clamp connections (Pl. XXVII, 11); nonamyloid. On various dead and living plant material, on dead insects, sand and humus, mosses, etc.; often in lawns and open woods on the ground, and more often on wood, but also on such substrata as dung, antesite, etc.). All species homothallic according to Kühner & Vandendries. Chemical reactions weak or none.

Developement of the carpophores: Unknown.

Area: Cosmopolitan.

Limits: The genus *Clitopilus* is easy to recognize for anyone who takes the trouble of checking on the peculiarly shaped spores, the lack of camp connections, and the sericeous cutis on the pileus. It is close to no other genus except *Rhodocybe*, and there most species are colored, or very bitter. It is less close to *Rhodophyllus* but has spores which are never angular when seen in profile or in frontal view. *R. candidissimus* which is similar in habit to some of the strongly pleurotoid, small *Clitopili*, differs by the peculiar spores and the presence of clamp connections.

Fayod originally distinguished two genera, *Octojuga*, and *Hexajuga*, and the combination of both these genera into a single one produced the modern genus *Clitopilus*. The author separated *Hexajuga*, from *Octojuga*, just as Fayod did, until, in 1942, he found that there are species intermediate between the two genera, and consequently no sharp dividing line can be discovered. He then joined Josserand who, somewhat earlier, had indicated the same opinion.

State of knowledge: The genus *Clitopilus* has recently been studied by two authors independently, neither knowing of the other's work because of the war conditions. Consequently, the general state of knowledge is comparatively satisfactory. We know now twelve species in this genus.

Practical importance: Some of the larger forms are often eaten. *Clitopilus prunulus*, though bitter forms are sometimes encountered, can, as a rule be considered as one of the best edible mushrooms. None of the *Clitopili* can be considered mycorrhizal on the basis of known facts or field observations. The wood destroying qualities of

some species are practically negligible. *C. Passeckerianus* is a weed fungus in white mushrooms cellars, but hardly damaging.

SPECIES

Sect. 1. **PRUNULI** (Quél. 1886) Sing. (1946). Carpophores medium sized to rather large, distinctly and persistently stipitate; spores with mostly 6 reinforced longitudinal angles, 10-14 μ long.

Type species: *C. prunulus* (Scop. ex Fr.) Quél.

C. prunulus (Scop. ex Fr.) Quél. [Paxillus, Quél. 1886; Hexajuga, Fayod; Rhodosporus, Schroter; Pleuropus, Murr.; Paxillopsis, Lange; Clitopilus orcellus (Bull. ex Fr.) Quél.; Pleuropus obesus Murr.] with a bitter tasting variety.

Sect. 2. **SCYPHOIDES** Sing. (1946). Carpophores rather small, scarcely medium sized, or else spores smaller than 10 μ in length; constantly and distinctly stipitate.

Type species: *C. scyphoides* (Fr.) Sing. (var. *typicus* f. *typicus*).

C. Giovanellae (Bres.) Sing. (Omphalia, Bres.); *C. scyphoides* (Fr. sensu Lundell & Nannfeldt) Sing. (Omphalia, Quel.; Agaricus mutilus Fr.; Pleurotus, Gillet; Clitopilus submicropus Rick; Omphalina floridana Murr.; Pleuropus minimus Murr.; Clitopilus omphaliformis Josserand; Agaricus cretatus Berk. & Br.; Clitopilus, Sacc.; Clitopilopsis, R. Maire; Clitopilus cretaceus R. Maire); this species consists of a series of varieties (see *Farlowia* **2**, 554-557. 1946), including one from India, thus far unpublished; *C. orcelloides* Pat. & Demange; *C. crispus* Pat.; *C. pusillimus* (Speg.) Sing. (Omphalia, Speg.).

Note: Josserand differentiates between the pleurotoid and the omphalioid form of what is here called *C. scyphoides*. In his opinion, *Agaricus mutilus* must be considered white spored, a deduction that is not forceful at all; also *Agaricus scyphoides* is, in opposition to the Scandinavian tradition, considered as doubtful, and excluded from *Clitopilus*. In Josserand's scheme, our *C. scyphoides* in the wider sense would therefore be replaced by the following two binomials: *C. cretatus* (Berk. & Br.) Sacc. and *C. submicropus* Rick (which has the priority over *C. omphaliformis* Josserand).

Sect. 3. **PLEUROTELLOIDES** Sing. (1943). Stipe inconstant, or not persistent, or rudimentary, or completely lacking.

Type species: *C. pleurotelloides* (Kühner) Josserand.

C. venososulcatus Sing.; *C. septicoides* (Henn.) Sing. (Pleurotus,

Henn.; Clitopilus pleurotelloides (Kühner) Josserand; Octojuga, Kühner; Octojuga Fayodi Konr. & Maubl.; Geopetalum viticola Mart.; Pleurotus, Coker; Crepidotus subversutus Peck apud Reid, nom. nud.; Pleurotus pusillus Speg.; Pleurotus Romellianus Pilát]; *C. Passeckerianus* (Pilát) Sing. (Pleurotus, Pilát; Pleurotellus, Konr. & Maubl.; Octojuga, Sing. 1942): *C. pinsitus* (Fr.) Josserand sensu Josserand; *C. incrustatus* Sing.; *C. filifer* (Speg.) Sing. (Pleurotus, Speg.); *C. argentinus* Sing.

KEY TO THE SPECIES

A. Carpophore medium to rather large; pileus 30–130 mm broad, fleshy, with the external appearance of a *Clitocybe* or *Paxillus involutus*; spores with six longitudinal furrows between six longitudinal folds or obtuse ridges, and therefore tri-striate when seen in profile, with (5–)6(7) angles when seen from one end; 7, 10–14 μ long. Growing on the ground. Temperate and subtropical zones of Europe, Asia, North Africa and North America. *C. prunulus*

A. Carpophore or spores smaller, usually between 7 and 9 μ long, but often as small as 5.5 μ or as long as 11.5 μ, with usually a larger number of angles than 6, most frequently 8, and often up to 10. Growing on the ground, or on various dead and living organic matter.

B. Stipe present, constantly persistent.

C. On horse manure in mushroom cellars; stipe very small, less than 3 mm long. *C. Passeckerianus*

C. Not on manure; stipe usually longer, or with bulb.

D. Pileus gray. *C. Giovanellae*

D. Pileus white.

E. Spores with scarcely projecting ridges or folds, merely angular when seen from one end. *C. scyphoides*, *C. pinsitus*

E. Spores with strongly (0.4 μ) projecting longitudinal ridges or folds. Indo-China.

F. Pileus fleshy, with crenate margin. *C. crispus*

F. Pileus thin with smooth, entire margin. *C. orcelloides*

B. Stipe absent, or spurious, or disappearing with age, or inconstant.

G. On horse manure, in white mushroom cellars (astipitate forms of *C. Passeckerianus*).

G. On substrata other than manure.

H. Pileus rugose-venose; growing on the wood of evergreen trees in tropical forest, Florida and south. *C. venososulcatus*

H. Pileus smooth, or transparently striate.

I. Pileus white or whitish, not cinereous. *C. septicoides*, *C. argentinus*, *C. filifer*

I. Pileus cinereous from an incrusting pigment. *C. incrustatus*

136. RHODOCYBE R. Maire

Bull. Soc. Mycol. Fr. **40**: 298. 1925, em.

Type species: *R. caelata* (Fr.) R. Maire.

Characters: Habit collybioid, clitocyboid, almost omphalioid, or tricholomatoid; pileus colored or more rarely whitish; epicutis consisting of radially arranged hyphae which are strictly elongate and repent; lamellae adnexed to decurrent, sometimes sinuate; hymenophoral trama much the same as in *Clitopilus*; basidia normal, 4 spored more rarely 1-2-3 spored; cheilocystidia not differentiated but pseudocystidia of a special type (colored, non lactiferous, not gloeocystidial) numerous, rooting in the lateral stratum (hymnopodium) or else continued by equally colored conducting elements that run parallel with the hyphae of the trama, or in other species without any such cystidia and conducting elements; spore print pink (to nearly fuscous or gray?), spores hyaline to pale stramineous, roughwarty, with moderately thin walls, without germ pore or callus, non amyloid, strongly angular when seen from one end (with the longitudinal axis vertical), and only a minority of spores showing a partially angular outline when seen in profile, or frontally; stipe present, central, evelate; context consisting of clampless, nonamyloid hyphae. On the ground or on débris.

Development of the carpophores: Unknown.

Area: Temperate and subtropical zone of both hemispheres, perhaps very widely distributed.

Limits: The delimitation with *Rhodophyllus* and *Clitopilus* is as pointed out in the key (p. 605). The author prefers to include those species of *Lepista* that have no clamp connections and (according to Kühner) binucleate spores.

State of knowledge: The species of *Rhodocybe* are rather well known. At present, we distinguish 12 species, and 2 subspecies.

Practical importance: Some of the species of *Rhodocybe* are edible, others are likely to be confused with edible ones, but cannot be used since they are very bitter.

SPECIES

Sect. 1. NITELLINAE (Sing. ut sect. *Rhodopaxilli*, 1942) Sing. External appearance similar to that of a *Hebeloma*, *Collybia*, or *Tri*

choloma. Pileus carneous ferruginous, light fulvous, brownish yellow, tan color, etc. Taste more often mild than bitter, pseudocystidia none.

Type species : Rhodopaxillus nitellinus (Fr.) Sing. (= *Rhodocybe nitellina*).

R. rosciavellanea (Murr.) Sing. (Pleurotus, Murr.); *R. truncata* (Schaeff. ex Fr.) Sing. (Hebeloma, Karst.) with its subspecies : *typica*, ssp. *mauretanica* (R. Maire) Sing. (Rhodopaxillus truncatus var. mauretanicus R. Maire) and ssp. *subvermicularis* (R. Maire) Sing. (Rhodopaxillus truncatus var. subvermicularis R. Maire); *R. alutacea* Sing.; *R. nuciolens* (Murr.) Sing. (Melanoleuca, Murr.); *R. nitellina* (Fr.) Sing. (Collybia, Quel.; Rhodopaxillus, Sing. 1939); perhaps also *R. Broadwayi* (Murr.) Sing. (if clamp connections absent).

Sect. 2. **DECURRENTES** (Konr. & Maubl. ut sectio *Rhodopaxilli*, 1924-37) Sing. External appearance like that of an *Omphalina* or *Clitocybe*. Pileus whitish, gray, or fuliginous; taste often very bitter, or moderately bitter; pseudocystidia none.

Type species : Rhodopaxillus mundulus (Lasch) Konr. & Maubl. (= *Rhodocybe mundula*).

R. mundula (Lasch) Sing. (Rhodopaxillus, Konr. & Maubl.); *R. popinalis* (Fr.) Sing. (Clitopilus, Gillet; Agaricus senilis Fr.; Agaricus Amarella Pers.); *R. noveboracensis* (Peck) Sing. (Clitopilus Sacc.); *R. fallax* (Quél.) Sing. (Omphalia, Quél.; Clitocybe, Sacc. & Trotter); *R. himantiigena* (Speg.) Sing.; probably also the species described by Ricken as « *Clitocybe parilis* (Fr.) » but this is possibly a species of the genus *Clitopilopsis* if the latter is accepted.

Sect. **GENUINAE** Sing. 1946 (*Rhodocybe* sensu originali). External appearance that of a small *Tricholoma* or *Clitocybe*; pileus brown or pale gray. Taste mild; pseudocystidia striking, colored, many of them projecting into the conducting system where the elements are also colored, not staining deep blue with 1 % watery solution of cresyl blue.

Type species : R. caelata (Fr.) R. Maire.

R. caelata (Fr.) R. Maire; *R. striatella* Kühner.

KEY TO THE SPECIES

A. Pseudocystidia present and very striking because of the bright color. Europe and North America. — *R. caelata* and *R. striatella*

A. Pseudocystidia none.

B. Stipe becoming hollow; taste usually mild; context of the cortex of the stipe cartilaginous or subcartilaginous; pileus never gray or fuscous-fuliginous or white; lamellae sinuate or adnate; habit collybioid

C. Lamellae broad; stipe thin; montane and boreal zones of the Northern Hemisphere. *R. vitellina*

C. Lamellae narrow; stipe comparatively thick. Western North America. *R. mucidolens*

B. Stipe solid; taste mild or bitter; context of the stipe not cartilaginous; pileus sometimes gray or fuscous fuliginous, or white, or some other color; lamellae sinuate-subdecurrent or decurrent; habit collybioid, clitocyboid, tricholomatoid, or omphalioid.

D. Taste mild.

E. Spores 8 µ long or longer. Florida. *R. roseiavellanea*

E. Spores 8 µ long or shorter.

F. Pileus hygrophanous; in tropical and subtropical forests (without conifers) in Florida. *R. alutacea*

F. Pileus non-hygrophanous or almost non-hygrophanous (subhygrophanous).

G. In North Africa, sometimes on roots of *Pinus halepensis*. *R. truncata* ssp. *mauretanica* and ssp. *subvermicularis*

G. In South America on wood, needles, cycads, etc. *R. himantiigena*

D. Taste bitter.

H. Pileus rosy-isabelline-fulvous or light flesh-color tawny (color of a *Hebeloma*). *R. truncata* (*typica*)

H. Color different.

I. Pileus 20-50 mm broad; brownish gray, grayish-alutaceous, initially convex, frequently umbonate, then infundibuliform; spores smaller than 6 µ; lamellae dark brown gray. In meadows, mostly in Europe. *R. popinalis*

I. Pileus either smaller or larger than indicated above (but often some carpophores falling within these limits), always paler than indicated above, and not combining all the characters indicated above. In the woods.

J. Pileus umbilicate or narrowly depressed, more rarely umbonate, dingy white; lamellae white, both the center of the pileus and the lamellae becoming gray on drying and sometimes also on injury: pileus 27-57 mm broad; odor of *Collybia dryophila*; base with strong coarse mycelial tomentum; spores short-ellipsoid, some smooth, some warty, most angular in end view, 5.5-6.3 × 3.8-4.8 µ; KOH with surface of pileus red « Arabesque », then « Couldron » (M. & P.) eventually dull brown. Mostly among leaves in and near the woods. From Maine south to North Carolina and west to Michigan. *R. noveboracensis*

J. Not combining all the characters indicated above. Species observed only in the eastern hemisphere

K. Pileus umbonate, 10-36 mm broad, odor reminiscent of *Clitocybe inornata;* taste moderately bitterish. Europe, Caucasus, North Africa. *R. fallax*

K. Pileus convex and obtuse, becoming infundibuliform, 30-70 mm broad, odor farinaceous; taste extremely bitter. Europe, Caucasus, and Siberia *R. mundula*

137. RHODOPHYLLUS Quél.

Enchiridion, p. 57. 1886.

Type species : R. lividus (Bull. ex Fr.) Quél.

Syn. : Acurtis Fr., *Summa Veg. Scan.* p. 337. 1849 [123].
Entoloma (Fr.) Quél., *Champ. Jura Vosges*, p. 116. 1872-73.
Agaricus tribus *Entoloma*, *Epicrisis*, p. 143. 1836-38.
Nolanea (Fr.) Quél., *l. c.* p. 122.
Agaricus tribus *Nolanea* Fr., *Syst. Mycol.* 1 : 204. 1821.
Leptonia (Fr.) Quél., *l. c.* p. 121.
Agaricus tribus *Leptonia* Fr., *Syst. Mycol.* 1 : 201. 1821.
Eccilia (Fr.) Quél., *l. c.* p. 123.
Agaricus tribus *Eccilia* Fr., *Syst. Mycol.* 1 : 207. 1821.

[123] The nomenclatorial situation is most confused as regards the genus *Rhodophyllus*. The genus *Acurtis* is undoubtedly based on the carpophoroids of *Rhodophyllus abortivus* (Peck) Sing. The author's own type studies reveal that type material preserved at the Farlow Herbarium, also seen and commented on by Burt (*Ann. Missouri Bot. Gard.* 7 : 68. 1922) is not a clavariaceous fungus but a sterile carpophoroid, and since the carpophoroid of *R. abortivus* is unique in the United States, the type cannot be anything else. There is a question as to whether the original diagnosis by Schweinitz was based on this exclusively. Schweinitz's description is so inadequate, and contains so strange data (« clavis compressis, contortis ; ... magnitudine capitis humani. Quandoque pulvere albo detergibili tegitur ») that one is tempted to think that Schweinitz included observations on other fungi. However, since the type does not contain other fungi, Art. 64 of the International Rules does not apply. Since the carpophoroids of this species (Pl. VI) are not necessarily monstrosities, the application of Art. 65 is also precarious. Since the carpophoroids are not a phase of a pleomorphic life-cycle, the application of Art. 57 is out of the question. This means that legally *Acurtis* would be the correct name for all species of *Rhodophyllus*, and unless the latter name is conserved, it will be replaced by *Acurtis*.

The question now is whether to propose *Rhodophyllus* or *Entoloma* or *Eccilia* for conservation. The author has repeatedly expressed his opinion that *Rhodophyllus* should at least be conditionally conserved. If such a conditional conservation is legally improper, this procedure should be made legal, or else *Rhodophyllus* must be conserved unconditionally.

Claudopus (Fr.) Gillet, *Champ.*, p. 426. 1876

Agaricus subgenus *Claudopus*, W. G. Smith, *Clavis Agar.*, p. 17. 1870.

Hyporrhodius Schroter in Cohn, *Krypt.-Fl. Schlesiens, Pilze* 1 : 613. 1889.

Latzinaea O. Kuntze, *Rev. Gen. Pl.* 2 : 857. 1891.

Leptonella Earle, *Bull. N. Y. Bot. Gard.* 5 : 424. 1909

Characters : Spores (Pl. XI, 5-6) with moderately thick to rather thin, simple, nonamyloid wall, usually angular and then with angular outline from all sides, from the ends (with the longitudinal axis vertical) as well as in profile, or frontally, pink in print (« rose beige 2 + » to « blush », or Plate 12, D 8 of Maerz & Paul); basidia normal or with carminophilous granulosity (according to Kühner), rather rarely 2-spored, but definite 2-spored races are in existence; cystidia absent or present, either only on or near the edges of the lamellae, or on the sides as well as on the edges; hymenophore lamellate in all normal forms; hymenophoral trama regular in the mediostratum, irregular and denser in an outer layer (hymenopodium); subhymenium consisting of very short elements; habit pleurotoid, mycenoid, collybioid, omphalioid, clitocyboid, or tricholomatoid; lamellae never quite free as in the *Amanitaceae;* hyphae nonamyloid, with or without clamp connections, sometimes intermixed with laticiferous hyphae; latex present in one species. On various substrata, even on carpophores of *Agaricales* and *Aphyllophorales*, also in deep moss, on cortex and wood, dead leaves, etc., most frequently on the soil.

Development of the carpophores: Gymnocarpous in the species studied by Douglas and Blizzard.

Area : Cosmopolitan, but most of the single species occupying very definite areas, and even some of the sections predominantly either temperate or tropical, etc.

Limits : The delimitation of the genus is quite obvious when the characters indicated in the key, p. 603, are carefully studied. Only two minor questions are interesting in this particular connection. These are :

(1) The delimitation of the forms of *Rhodophyllus* with non angular spores from the genera of other families, sharing some essential characters with them. In the first place, these non-angular spores are very rare in *Rhodophyllus*, and where they occur, they often reveal themselves by depositing spore prints containing at least some angular spores. But even if they do not contain any angular spores, they can be distinguished from other genera with pink spore print, if care is taken not to make any determinations with a sche-

matic state of mind. This means that any species with pink spore print that is isolated in the group where it would key out because of non angular spores, should be judged by other, secondary characters, such as the presence or absence of clamp connections, the diameter and firmness of the wall of the spores, etc. The *Rhodophylli* have a rather characteristic stramineous, moderately thick spore wall that is not known in many of the other pink spored groups. The *Amanitaceae* are immediately excluded because of the structure of their hymenophoral trama. The *Tricholomataceae* with pink spores have clamp connections more often than not, whereas the smooth-spored *Rhodophylli* rarely have clamp connections. The species still not recognizable, if all these data are taken into consideration, are surely theoretical because the author does not know any such case. If it should come up during future taxonomic work, other secondary characters, not agreeing with the genus where they would key out in formal determination, will be pointed out. In all cases, the affinity with some of the typically angular spored forms will decide the issue in favor of *Rhodophyllus* for all experienced taxonomists.

(2) The position of *« Pleurotus » candidissimus.* This is a very peculiar small pleurotoid fungus, remarkable for its small, moderately strongly angular spores, and its clamp connections. The author believes that at the present time there is no better place for this fungus than the genus *Rhodophyllus*, subgenus *Eccilia.*

State of knowledge : Nearly 600 species have been described by the various authors in a more or less complete way. Out of this total, the author recognizes now 106 species which according to the data available are known well enough to be inserted in Romagnesi's classification of the genus. The author has attempted to follow Romagnesi as closely as possible since his papers are the only modern treatments available. Romagnesi published two important papers, aside from several smaller ones, on the *Rhodophylli* of Europe and Africa [124]. These papers represent a remarkable progress in our knowledge of the *Rhodophylli*, and, as far as the spore characters are concerned, as well as in the evaluation of the characters based on the habit (and borrowed from the classification of the white-spored agarics as introduced by Fries), it is based on a new and very

[124] Romagnesi, H., *Essai d'un sectionnement du genre Rhodophyllus. Bull. Soc. Myc. Fr.* **53** : 319. 1937 ; and id., *Prodrome a une flore mycologique de Madagascar II. Les Rhodophyllus de Madagascar.* Paris 1941.

interesting approach. There are merely a few minor questions concerning the application of the rules of nomenclature where the author was unable to accept Romagnesi's results. As for the *Rhodophyllus* flora of such regions as Asia and America, Australia or West Africa, there is still a wide field for careful comparative and analytical type studies. There is no lack of validly published binomials, and many of them are backed up by type specimens in good condition. This is especially true for the species from North America, partly also South America, West Africa, and tropical Asia.

It also appears, according to the limited experience of the author, that a list of all those species possessing clamp connections, and another one containing those lacking them, would be an interesting check on the present classification. The same is true for the carminophilous granulosity of the basidia (*Lyophyllum* basidia) which is said to occur in *Rhodophyllus*. If one or both of these characters would prove to be correlated with those stressed by Romagnesi's classification, it would enormously strengthen the latter and simplify the large task of classifying hundreds of species which are thus far incompletely known. The author has notes on species which are constantly provided with clamp connections and others that never have any, but the material concerned is too limited in number to be of any value on a larger scale. The author's notes show that certain species react very strongly with monomethylparamidophenol (e. gr. *R. abortivus*) whereas others give a rather weak reaction. This reagent may be useful for the identification of certain species in the field, or as an additional taxonomic character. Only systematic studies on these problems will show whether they have possibilities for the systematist.

Practical importance: Some species are edible. A few are even sold in the markets of Europe and Asia. For every good edible species, there seems to be one poisonous species of *Rhodophyllus*. Among them, *R. sinuatus* is the only truly dangerous species. Other weakly poisonous species seem to be limited to the group of *R. rhodopolius*.

The genus *Rhodophyllus* is probably not represented among the typical selective mycorrhizal fungi, or at least this is the impression of a field observer, and no conclusive evidence to the contrary has been offered by experimental workers.

SPECIES

Note : In the second paper cited above, Romagnesi changed his original classification to a considerable extent, and the author published an outline of his own classification (essentially based on a correspondence between him and Romagnesi) in 1942 and 1943. The following classification is a synthesis between these three classifications proposed thus far. They are all in Romagnesi's spirit, and coincide most closely with his latest paper — safe for a few exceptions which are pointed out in foot notes below.

I. SERIES OF SUBGENERA WITH SYMMETRICAL SPORES (PL. XI, 6)

Subgenus I. **Eccilia** (Fr.) Quél. (1886) em. Sing. (1942) (*Agaricus*, trib. *Eccilia* Fr. 1821)[1]. Pileus depressed, rarely umbonate-papillate and then lamellae at least subdecurrent; stipe either fragile and subcartilaginous, or rather soft, fleshy, and then often eccentric or strongly reduced; small fungi, usually with thin context.

Type species : Agaricus (*Eccilia*) *parkensis* Fr. (*Rhodophyllus parkensis*).

Sect. 1. TRIGONOPHYLLI Romagnesi (1938). « Typical habit of *Eccilia* ; pileus more or less depressed in the center, dull colored, brown, blackish brown, etc... Stipe slender, mostly elongate; size

[1] This subgenus combines the primitive groups of the series with symmetric spores, distributed, in Romagnesi's last paper (1941), among the subgenera *Leptonia* and *Hydropilus*. The author does not think that this reorganization of groups alters much in Romagnesi's general scheme. Unfortunately for the author's purpose of keeping as closely to Romagnesi's nomenclature as is consistent with the author's own views and with the strict compliance with the International Rules of Nomenclature, the sections used by Romagnesi are not accompanied by Latin descriptions. Since the author had no knowledge of Romagnesi's second paper when publishing his tentative outline of classification in 1942-43, Romagnesi's names could not be anticipated. Besides, the absence of indications regarding the type species of the various subdivisions proposed by Romagnesi, often makes it difficult to apply the scheme of typification published by Singer & Smith (*Mycologia* 38 : 240-299 (1946) to these units. These are the reasons behind some minor changes, e. gr. the nomen novum introduced to replace Romagnesi's subgenus *Nolanea* which is not that of Fries as defined by the lectotype adopted by Singer & Smith according to the general principles laid down in the introduction to the paper of these authors

small; general appearance slender. Lamellae distant, arcuate decurrent and triangular. » Romagnesi.

Type species: As in the subgenus.

R. parkensis (Fr.) Quel. Probably some more species will be added in the future.

Sect. 2. MINUTI Romagnesi (1938). Like the preceding section but still smaller (never larger than 10 mm), whitish with deep colored papilla and transparent striae; stipe filiform, not always as typically *Eccilia*-like in habit as the *Trigonophylli*.

Type species. *R. minutus* (Karst.) Lange

R. minutus (Karst.) Lange; *R. rhodocylix* (Lasch) Quél., and two species indicated by Romagnesi from tropical Africa: *R. granulatus* Romagnesi and *R. punctatulus* Romagnesi.

Sect. 3. UNDATI Romagnesi (1938). « Habit of *Clitopilus* or *Claudopus* [i. e. clitocyboid or pleurotoid], [those species with central or subcentral stipe, having rather fleshy carpophores and unicolorous and dull (grayish, brownish) pigmentation [if pigmented at all]. Stipe short, or even none, or lateral. Covering layer finely silky. Lamellae close, in general deeply decurrent, concolorous.» Romagnesi.

Type species: R. undatus (Fr.) Quél.

Subsection A. Stipe central or subcentral: *R. undatus* (Fr.) Quél.; *R. tortilis* Romagnesi; *R. Blandfordii* (Henn.) Sing. Eccilia, Henn.).

Subsection B. [128] This is the old genus, subgenus, or section *Claudopus* with strongly reduced stipe and medium sized to large spores. It includes the following species: *R. depluens* (Pers.) Quel.; *R. byssisedus* (Pers. ex Fr.) Quél.; *R. lazulinellus* Sing. (Pleurotus lazulinus Speg.); *Rhodophyllus cyaneus* (Murr.) Sing.

Subsection C. This is characterized by the extremely small spores [129].

The only species known is *R. candidissimus* (Berk. & Curt.) Sing. (Pleurotus, Sacc.; Pleurotellus, Kour. & Maubl.).

Sect. 4. CANDIDI (Romagnesi 1938 ut subsectio) Romagnesi (1941). Pileus and stipe pure white; stipe always well developed; otherwise much like the preceding sections.

[128] Future classifications may raise this subsection to an autonomous section characterized by pleurotoid habit, white gray or blue color, absence of carminophilous granulation in the basidia, and presence of clamp connections in all hyphae.

[129] This subsection may also be expected to be raised to the status of a section in future classifications of the genus.

Type species: R. sericellus (Bull. ex Fr.) Quél. sensu Boudier.

R. sericellus (Bull. ex Fr.) Quél. sensu Boudier; *R. carneoalbus* (With. ex Fr.) Quél.; *R. truncatus* Romagnesi; *R. albellus* Romagnesi; *R. subsericellus* Pat. (R. platypus Romagnesi); perhaps *R. stylophorus* (Berk. & Br.) Romagnesi (R. cuspidatus Pat. non al.).

Subgenus II. **Romagnesia** Sing. (1943). Pileus either not depressed, or if it is depressed at maturity, the context is thick and fleshy and the stipe is also thick and firm; pigments of a dull (brown, gray, olive-fuscous) color, never bright colored.

Type species: R. clypeatus (L. ex Fr.) Quél.

Sect. 5. POLITI (Romagnesi 1938 ut subsectio) Sing. (1943). Lamellae rather strongly decurrent.

Type species: R. politus (Fr.) Quél.

R. politus (Fr.) Quél.; *R. Woodianus* (Peck) Romagnesi; *R. abortivus* (Berk. & Curt.) Sing. (Clitopilus, Sacc.); *R. albogriseus* (Peck) Sing. (Clitopilus, Sacc.), etc.

Note: It seems that many species of the genus *Pleuropus* as interpreted by Murrill l. c. will probably enter this section. This section is transient between the preceding subgenus and the subgenus *Romagnesia*.

Sect. 6. RHODOPOLII (Fr. 1821 ut subtrib.) Romagnesi (1947). Lamellae not decurrent; habit usually more or less tricholomatoid.

Type species: R. rhodopolius (Fr.) Quél.

R. ameides (Berk. & Br.) Quél.; *R. nidorosus* (Fr.) Quél.; *R. rhodopolius* (Fr.) Quél. *R. pseudoexcentricus* Romagnesi; *R. turbidus* (Fr.) Quél.; *R. vetulus* Romagnesi; also possibly *R. costatus* (Fr.) Quél.; *R. elaphinus* (Fr.) Quél.; *R. majalis* (Fr.) Quél.; *R. radiatus* Lange; *R. Cordae* (Karst.) Lange; also many American species, among others *R. strictior* (Peck) Sing. [Entoloma strictius (Peck) Sacc.]; *R. Grayanus* (Peck) Sing. [Entoloma (Peck) Sacc.]; *R. Westii* (Murr.) Sing. (Entoloma Westii Murr.).

Subgenus III. **Paranolanea** Sing. n. n. (*Nolanea* sensu Romagnesi 1941). Pileus conical, often papillate, non hygrophanous, either fibrillose-squamulose as in *Inocybe*, or with a palisadic cuticle, or with bright (blue, green, etc.) pigment; spore wall remarkably thick; lamellae subfree to sinuate. Mostly tropical.

Type species: R. psittacinus Romagnesi.

Sect. 7. VERSATILES Romagnesi (1938, nom. nud.; 1941). « Pileus conical or campanulate fibrillose or even squamulose, rarely subglabrous, non hygrophanous; lamellae rarely adnate, mostly free

or ventricose. Almost always with pleurocystidia... External appearance of *Inocybe.*» «Incrusting pigment present.» Romagnesi.

Type species : R. versatilis (Fr. sensu Ricken) Quél.

R. versatilis (Fr. sensu Ricken) Quél.; *R. araneosus* Quél.;

Sect. 8. INOCEPHALI Romagnesi (1947). African species similar to sect. 7 but with vacuolar pigmentation.

Type species : R. inocephalus Romagnesi.

P. Peckianus (Burt in Peck) Romagnesi sensu Romagnesi (from Madagascar); *R. inocephalus* Romagnesi; *R. coprinoides* Romagnesi; *R. hirtellus* Romagnesi; *R. Heimii* Romagnesi.

Sect. 9. LAETI Romagnesi (1941). «Habit of *Nolanea.* Pileus conical, often papillate, generally finely silky fibrillose, non-hygrophanous, always of agreeable and light colors (yellowish, tawny, pink, etc.). Stipe rather slender, often striate but not canaliculate. Lamellae adnate decurrent or subfree, of light color; cheilocystidia frequent.» Romagnesi.

Type species : R. camaroensis (Bres.) Romagnesi.

R. kameruunensis (Bres.) [14] Sing. (Nolanea, Bres.); *R. rhodellus* Romagnesi; *R. phleboides* Romagnesi; possibly *R. rhodurus* (Gilbert) Romagnesi; *R. icterinus* (Fr.) Quel.; *R. Bigeardii* (Barbier) Romagnesi; *R. campanulatus* Romagnesi; *R. nigropapillatus* Romagnesi.

Sect. 10. PSITTACINI Romagnesi (1941). «Pileus conical, pointed-acute, often papillate. Stipe robust, deeply channeled. Lamellae thick, free, ascendant, ventricose. Strongly colored blue, green, red, even inside. All hyphae strongly pigmented. Spores cubic. Clavate cheilocystidia frequently present. Context sometimes lactescent, and then with a ringlike thickening of the stipe. External appearance of a *Hygrocybe* of the section *Conicae.*» Romagnesi.

Type species : R. psittacinus Romagnesi.

R. psittacinus Romagnesi; *R. holocyaneus* Romagnesi; *R. lactifluus* Heim; *R. cubisporus* Pat. At the Farlow Herbarium is an unpublished species collected by D. H. Linder in British Guiana which belongs in this section.

Sect. 11. CALLIDERMI Romagnesi (1941). Pileus conical, then repand papillate, blue in the type species. Cuticle of palisade structure, consisting of fusiform cells; hypodermium differentiated, consisting of loosely interwoven hyphae.

[14] The original spelling is *Nolanea kameruunensis* Bres. (*Bull. Soc. Myc. Fr.* 6: xxxiv. 1890). The same spelling is on plate I. Hennings' *Eccilia cameruunensis* must be renamed, if transferred to *Rhodophyllus.*

R. callidermus Romagnesi.

Subgenus IV. **Leptonia** (Fr.) Quél. (1816), em. Romagnesi (1941). Pileus umbilicate, with more or less squamulose umbilicus, or, if glabrous, either non hygrophanous, and then often with dull colored pigment, or hygrophanous. Lamellae not deeply decurrent and not at the same time distant and adnate, at least if the pileus is fibrillose.

Type species : R. anatinus (Lasch) Quél.

Sect. 12. SOLSTITIALES (Romagnesi ut subsectio) Sing. st. n. Pileus glabrous, non hygrophanous.

Type species : R. solstitialis (Fr.) Quél.

R. solstitialis (Fr.) Quél. sensu Ricken ; *R. Sphagnorum* Romagnesi & Favre ; *R. subglaber* Romagnesi ; possibly also *R. incertus* Romagnesi.

Sect. 13. FULIGINOSI (Romagnesi ut subsectio) Sing. st. n. Pileus usually squamulose or fibrillose, hygrophanous or non-hygrophanous ; pigment dull colored, dusky fuscous or gray ; lamellae adnate.

Type species : R. aethiops (Fr.) Quél.

R. aethiops (Fr.) Quél. ; *R. atromarginatus* Rogmagnesi & Favre ; *R. pardinus* Romagnesi ; *R. subsquamosus* Romagnesi ; *R. geminus* Romagnesi.

Sect. 13*a*. Pileus strongly pilose (Pl. XV, 3) as in *Crinipellis ; R. squamifolius* (Murr.) Sing. (Crinipellis, Murr.).

Sect. 14. LEPTONIARII Romagnesi (1938), em. Pileus squamulose, non hygrophanous, pigments bright.

Type species : R. serrulatus (Pers. ex Fr.) Quél.

R. serrulatus (Pers. ex Fr.) Quél. ; *R. griseocyaneus* (Fr.) Quél. ; *R. asprellus* (Fr.) Quél. ; *R. catalaunicus* (Sing.) Romagnesi ; *R. Queletii* (Boudier) Quél. ; *R. infundibularis* Romagnesi ; *R. hypoglaucus* Romagnesi ; *R. iodes* Pat. ; *R. atroviolaceus* Romagnesi ; obviously also *R. anatinus* (Lasch) Quél. and *R. placidus* (Fr.) Quél.

Sect. 15. FRAGILES Romagnesi (1938). Pileus hygrophanous ; either green or yellow.

Type species : R. euchlorus (Lasch) Quél.

R. euchlorus (Lasch) Quél. ; *R. Whiteae* (Murr.) Heim & Romagnesi ; *R. formosus* (Fr.) Quél.

II. SERIES OF SUBGENERA WITH ASYMMETRICAL SPORES

Subgenus V. **Paraleptonia** Romagnesi (1941). Pileus glabrous or silky with involute margin, infundibuliform, depressed or umbilicate. Lamellae decurrent or adnate.

Type species: R. sarcitus (Fr.) Quél.

Sect. 16. SARCITI Romagnesi (1941). « Habit of *Leptonia* or *Clitopilus*. Colors dusky or dark, gray, brown, etc. Lamellae decurrent or adnate, mostly grayish. » Romagnesi.

Type species: R. sarcitus (Fr.) Quél.

R. sarcitus (Fr.) Quél.

Sect. 17. CANCRINI Romagnesi (1938). « Habit of *Eccilia* (or *Nolanea*). Pileus pure white or pale yellowish, non hygrophanous, more or less strongly fibrillose silky. Lamellae initially white. » Romagnesi.

Type species: R. cancrinus (Fr.) Quél.

R. cancrinus (Fr.) Quél.; *R. rhodanthes* Romagnesi, and perhaps *R. pleopodius* (Bull. ex Fr.) Quél.

Sect. 18. OLORINI Romagnesi (1941). « Habit of *Clitopilus* or *Eccilia*. Pileus depressed to infundibuliform, glabrous or silky. Color white or yellowish. » Romagnesi.

Type species: R. olorinus Romagnesi & Favre.

R. olorinus Romagnesi & Favre; *R. palleus* (R. Maire) Romagnesi (?).

Subgenus VI. **Nolanea** (Fr.) Romagnesi sensu Singer (1942). Pileus non viscid, non fibrillose and naked, conical, campanulate or convex, often umbonate. Lamellae subfree or sinuate adnexed, often ascendant or ventricose. Pigment of dull dusky shades, gray, fuscous, etc., or else yellow to orange. Stipe rather thin, very fragile or subcartilaginous to waxy. Pileus usually also thin and fragile.

Type species. Nolanea pascua (L. ex Fr.) Quél. [1].

Sect. 19. PASCUI Romagnesi (1938). « Typical *Nolanea* habit. Pileus conic or campanulate, sometimes eventually expanded, not

[1] This species has been split into several species by Romagnesi. Whether a lectotype is selected for it, or not (whereby it may become a nomen ambiguum), it must be assumed that it belongs entirely in this subgenus, also according to Romagnesi who named a section within this same subgenus after *Nolanea pascua*: section *Pascui* Romagnesi, the type of which must be *R. pascuus* in the sense of Romagnesi whatever that may be.

depressed, hygrophanous, becoming pallid and silky on drying, brown or somewhat tawny, rarely with brighter colors, whitish, etc. Stipe thin, cartilaginous, subconcolorous or whitish, longitudinally striate. Lamellae ascendant, subfree... »

Type species : R. pascuus (L. ex Fr.) Quél. sensu Lange (sensu Romagnesi p. p. ut. syn.).

Subsection **Staurospori** Romagnesi (1938). Spores prismatic.

Type species R. staurosporus (Bres.) Lange.

R. staurosporus (Bres.) Lange ; *R. xylophilus* Lange.

Subsection **Mammosi** Romagnesi (1938) Spores asymmetric-simple, or complex.

Type species : R. hirtipes (Schum. ex Fr.) Lange.

R. hirtipes (Schum. ex Fr.) Lange ; *R. mammosus* (Fr.) Quél. ; *R. clandestinus* (Fr.) Quél. (sensu Bres.) ; *R. metulus* Romagnesi ; probably also *R. coeles* (Fr. sensu Ricken) Quél.

Subsection 3. As a third subsection one may temporarily add here the group of bright colored species (with yellow to orange red pigment) such as *R. Murraii* (Berk. & Curt.) Sing. [Entoloma cuspidatum (Peck) Sacc.] ; *R. salmoneus* (Peck) Sing. (Entoloma, Sacc.).

Sect. 20. **SPHAEROSPORI** Romagnesi (1938). « Habit of *Nolanea* or of the *Nolanea* like Entolomas. Pileus campanulate or convex, hygrophanous, of dark colors. Stipe slender and concolorous. Lamellae grayish, of dirty pinkish brown color when mature. Often inhabiting marshes and bogs. » Romagnesi.

Type species : R. sericeus (Bull. ex Fr.) Quél.

R. sericeus (Bull. ex F.) Quél ; *R. proletarius* (Fr.) Quél. (sensu Ricken) ; *R. paludosus* (Vel.) Romagnesi ; perhaps *R. juncеus* (Fr.) Quél.

Subgenus VII. **Entoloma** (Fr.) Romagnesi (1941). Pileus squamulose-fibrillose, or viscid, or at least with an epicuticular layer consisting of filamentous hyphae as in the viscid species. Pigment bright colored, violet, blue, green, etc., or black, or if not distinctly so colored, either the pileus and the stipe deep brown, or almost no pigment is present in the carpophores, or the habit is truly tricholomatoid. Cystidia on the sides of the lamellae none. Stipe thin, or thick and fleshy. Pileus thin and fragile, or thick and comparatively firm.

Type species : R. lividus (Bull ex Fr.) Quél.

Sect. 21. **LUCTUARII** Romagnesi (1938). « Habit of *Nolanea* or *Entoloma*. Pileus and stipe of dark colors, bister brown or black

ish, mostly fibrillose or even squamulose, hygrophanous or non-hygrophanous. Lamellae gray or brown, not much pinkish tinge visible on the mature ones. Cheilocystidia frequently present. » « Pigment membranal or incrusting. » Romagnesi.

Type species : R. Babingtonii (Blox.) Quel.

R. Babingtonii (Blox.) Quel. ; *R. fumosellus* (Winter) Lange ; perhaps also such species as *R. subnigrellus* Romagnesi ; *R. dysthales* (Peck) Romagnesi sensu Romagnesi ; *R. tigrinellus* Romagnesi; *R. leptohyphes* Romagnesi ; *R. rotula* Romagnesi ; *R. elongatus* Romagnesi.

Sect. 22. **LEPTONIDEI** (Fr. 1836) em. Romagnesi (1947). As sect. 21 but pigment vacuolar.

Type species : R. jubatus (Fr.) Quél.

R. jubatus (Fr.) Quél. ; *R. porphyrophaeus* (Fr.) Quél. ; *R. inutilis* (Britz.) Romagnesi.

Sect. 23. **EXCENTRICI** Romagnesi (1938), em. (1941). Pileus light colored (white), not violet, green, etc. Lamellae white ; cuticle composed of interwoven hyphae.

R. excentricus (Bres.) Romagnesi.

Sect. 24. **SPECULARII** Romagnesi (1941). « Pileus and stipe pure white, context scarcely hygrophanous ; cuticle not viscid but covered with an epicutis of fine filamentous hyphae as in the viscid species (see following section). Cystidia none. » Romagnesi.

R. speculus (Fr.) Quel.

Sect. 25. **GENUINI** [34] Fr. (1836) (*Viscosi* Romagnesi 1938). Pileus viscid, with an epicutis consisting of fine, filamentous hyphae which are more or less gelatinized, more or less erect or ascending, soft and thin-walled, very loosely interwoven.

Type species : R. lividus (Bull. ex Fr.) Quél. (*R. sinuatus*).

R. sinuatus (Bull. ex Fr.) Sing. (Agaricus lividus Bull. ex Fr. non Pers. ex Schwein, Secr. ; Rhodophyllus, Quél.) ; *R. prunuloides* (Fr.) Quél.; *R. plebejus* (Kalchbr.). Romagnesi; also perhaps some doubtful species, e. gr. *R. giganteus* (Murr.) Sing. (Entoloma, Murr.).

Sect. 26. **NITIDI** Romagnesi (1938). Pileus large or medium sized, fleshy, convex ; pigment black, blue, violet, porphyry, green, i. e. colors either very deep or very bright ; gelatinous epicuticular hyphae absent.

[34] It appears that the type of the genus or subgenus *Entoloma* should also be the type of the section *Genuini*. The section *Leptonidei* is based on *A. jubatus* as recognized by Romagnesi since 1947. The section *Nolanidei* Fr. = *Cypeati* Romagnesi is based on *A. clypeatus*

R. nitidus Quél.; probably also belonging here: *R. madidus* (Fr.) Quél.; *R. caelestinus* (Fr.) Quél.; *R. Bloxamii* (Berk.) Romagnesi; *R. violaceus* (Murr.) Sing. [Entoloma cyaneum (Peck.) Sacc.].

KEY TO THE SPECIES

The papers by Romagnesi and also Lange, *Flora Agaricina Danica* vol. I contain analytical keys. The author is not in a position to improve these keys.

GENERA INCERTAE SEDIS

Clitopilopsis R. Maire, *Publ. Inst. Bot. Barcelona* **3** (4): 82. 1937. (*Hirneola* Vel., *Nov. Myc.*, p. 73, 1939, non Fr.). « Spore print rose color; spores smooth; lamellae more often decurrent than ventricose adnate, not free; gill trama regular (not inverse); differing from *Clitopilus* in non costate spores ». R. Maire. The type species is *Clitopilopsis arthrocystis* Kühner & Maire which is a new name for *Clitocybe xanthophylla* Vel. (1920) from Czechoslovakia. In a recent paper, Kühner (*Bull. Soc. Myc. Fr.* **62**: 1 11. 1946) identifies *C. arthrocystis* with what he now calls *Clitopilopsis hirneola* (Fr.) Kühn. but describes the spore print as « d'un gris brun en demi masse » which is not in accord with Maire's original description which was more precisely meant to accomodate, aside from *C. arthrocystis* such species as *Clitopilus togoensis* Henn. These are of uncertain position, and the genus proposed by Maire must be accepted on the basis of the type concept, i. e. for any group of agarics that can be typified by *C. arthrocystis*. Since the author thinks that it is quite possible to consider this species as merely a smooth-spored *Rhodophyllus* [111] and Kühner claims that it is the representative of a genus (*Clitopilopsis*) closely related to *Rhodocybe* and *Clitopilus*, there can at least be no doubt as to the unanimity of the authors considering the position of this form in what is here called the family *Rhodophyllaceae* (partly equalling tribus *Orcellés* of Kühner). Kühner indicated that the spores are very slightly « facettées », i. e. angular in end view. This would indicate a closer

[111] This opinion quoted by R. Kühner l. c. has not by any means been demonstrated to be inacceptable in spite of the fact that Kühner contents himself with the single phrase « ce que nous ne pouvons admettre ». He confines himself to the question whether or not *Clitopilopsis* is close to *Rhodocybe*, and quite correctly

relationship with *Clitopilus*. If this shape of the spores is disregarded because of its indistinct character, it is then a question whether the absence of roughness should be disregarded and the fungus be considered as *Rhodocybe*, or the absence of angular outlines should be dismissed as unessential and the species be incorporated in *Rhodophyllus*. All three genera are already so close that it is possible to argue in favor of combination into a single genus. Kühner wants a genus *Clitopilopsis* recognized on the basis of the smoothness of the spores. Thus, instead of having three genera in the *Rhodophyllaceae*, Kühner would admit nine genera (*Clitopilus*, *Octojuga*, *Clitopilopsis*, *Rhodocybe*, *Entoloma*, *Leptonia*, *Nolanea*, *Eccilia*, *Claudopus*), or at least *Clitopilus*, *Clitopilopsis*, *Rhodocybe* and *Rhodophyllus*. Kühner also thinks that the genus *Lepista* is closely related with *Clitopilopsis*, a view the author used to share with Kühner formerly, but evidence quoted in various papers since then, has induced him to disagree now. *Lepista* is much closer to *Clitocybe* than to *Rhodocybe* in the author's opinion.

The only fact that might substantiate the claim to generic autonomy for *Clitopilopsis* would be the existence of a correlated character distinguishing this genus from the other genera of the *Rhodophyllaceae*. Then, on the basis of this character in addition to the smoothness of the spores, it might appear desirable or necessary to recognize *Clitopilopsis*. It is just possible that the exact color of the spore print or the study of the early development of the carpophores might provide such a character. Unless the color of the spore print in color chart terms and a detailed development study are available, *Clitopilopsis* cannot be recognized as an independant genus.

As for more detailed descriptive data on *Rhodophyllus* (or *Clitopilopsis*) *hirneolus*, the reader is referred to type studies published by the author (*Lloydia* **5**: 100. 1942), and Kühner's paper cited above.

PAXILLACEAE R. Maire, apud Maire, Dumée & Lutz

Bull. Soc. Bot. Fr. **48**: ccxliii. 1901 (*nom. nud.*); *Recherches*, p. 165. 1902 (ut Paxillacées); Lotsy, *Vorträge*, p. 716. 1907.

Type genus: *Paxillus* Fr.

Characters: Pileus subtomentose to tomentose, sometimes viscid, small to large, the margin initially involute; hymenophore lamellose but the lamellae frequently connected by anastomosing veins and

ridges, or the sides of the lamellae venose-rugose, more rarely the anastomoses broad and numerous and the hymenophore resembling that of *Merulius*, or else lamellae not intervenose but repeatedly forked; lamellae usually rather narrow, brownish, light tan, yellow, or orange, decurrent if a stipe is present; spore print from nearly white to « chamois » (Ridgway) or « oak » even « Coffee » or between « Alamo » and « Cocoa » (Maerz & Paul) (exact color unknown in *Linderomyces*); spores small to medium, smooth, or echinate, or verruculose uneven, ovoid, or ellipsoid, or globose, or ellipsoid oblong; cystidia present in one species of *Paxillus*; cosmocystidia present in *Linderomyces*; otherwise cystidia and pseudocystidia absent on the sides of the lamellae; hymenophoral trama more or less bilateral, i. e. either truly diverging in the lateral stratum, or with a regular mediostratum and a very interwoven intermixed, quite irregular lateral stratum which may diverge slightly near the edge of the lamellae; stipe present or absent, central, eccentric or lateral, without pseudorrhiza; hyphae with clamp connections (except for one unpublished species from Tierra del Fuego), intermixed with coscinoids in *Linderomyces*, all walls nonamyloid; veil present in *Paxillus argentinus*, otherwise absent; context usually strikingly soft and the hyphae somewhat subgelatinous in the trama of many species. On wood and on the earth, not forming mycorrhiza (at least no obligatory mycorrhiza connection observed). Chemical reagents, such as iron compounds, KOH, NH_4OH, etc. usually provoking strong color reactions on the surface of the carpophores and on the context (except in the orange species with repeatedly forked lamellae).

Limits: The *Paxillaceae* are close to the *Boletaceae* and the two preceding families. Their separation from the preceding families has been discussed there. As for the *Boletaceae*, the affinity is most obvious if the genus *Gyrodon* is compared with the genus *Paxillus*. Aside from the more individualized lamellae — even if they are connected by anastomoses —, the more involute margin of young specimens and the absence of true mycorrhizal relationships with forest trees separate the *Paxillaceae* from the *Boletaceae*. There is also a slight but distinct difference in the chemical reactions of *Gyrodon* and *Paxillus*. The greenish yellow color of the hymenophores in *Gyrodon* is indicative of its close affinity with the *Boletaceae*. There is also, in some species of *Gyrodon*, the blue discoloration caused by autoxidation of the hymenophore and the flesh when broken. This reaction is, although not a constant feature of all the

species of *Gyrodon,* a character common to many species of the *Boletaceae* whereas in the *Paxillaceae* this blue discoloration is constantly absent. Instead, there is a brown discoloration in *Paxillus involutus* and perhaps also some other species of this family. Furthermore, there appears to be a slight difference between the structure of the tube walls of *Gyrodon* and the trama of the lamellae in *Paxillus.* In the former, the mediostratum is somewhat denser and somewhat colored whereas the lateral stratum is distinctly divergent and hyaline in young material. In *Paxillus panuoides,* we find the lateral stratum, or as we would prefer to call this layer, the hymenopodium, strongly interwoven and not clearly diverging in all its parts in mature material. This layer looks so entirely different from the lateral stratum of *Gyrodon* that it is possible to consider it as non homologous. Instead, the homology is obviously with the hymenopodium of the *Rhodophyllaceae* (e. gr. the intermixed brown hymenopodium of *Rhodophyllus squamifolius*), the *Gomphidiaceae* (e. gr. the intermixed irregular hymenopodium of *Gomphidius rutilus*), etc.

The *Paxillaceae* are also close to the *Cortinariaceae,* since *Neopaxillus* belongs in the *Paxillaceae.* This genus is inserted in the *Paxillaceae* by virtue of its decurrent lamellae which give it the habit of a small *Phylloporus rhodoxanthus,* the ornamentation of the spores which is different from the type of ornamentation observed in the *Cortinariaceae* (*Cortinarius, Gymnopilus,* etc.), and the structure of the hymenophoral trama.

The genus *Hygrophoropsis* has been considered as belonging to the *Cantharellaceae,* the *Leptotaceae,* the *Tricholomataceae,* and finally, it was transferred by the author to the *Paxillaceae.* This was done in view of the close affinity that the author (1946) was able to demonstrate between *Paxillus Curtisii* and *Hygrophoropsis Tapinia.* In fact, there is now no difficulty in proving the fact that *Hygrophoropsis* and *Paxillus* are related. The difficulty consists in the delimitation of the *Paxillaceae* (*Hygrophoropsis*) rather than in the determination of the position of *Hygrophoropsis.* However, it can be stated that the repeatedly forked lamellae, the soft consistency — reminiscent of the *Boletaceae* and *Gomphidiaceae* as well as the *Paxillaceae* — and the non-amyloid spores represent a combination of correlated characters that make this genus well separable from the *Tricholomataceae.* In addition, the colors of the well known species of this genus are so characteristic that they, in addition to the characters mentioned above, make this genus very distinctive. The other agarics with repeat-

edly forked lamellae and fleshy consistency (*Russula cyanoxantha,* one form of *Leucopaxillus albissimus,* and *Cantharellula umbonata*) differ sharply from *Hygrophoropsis* because of the amyloid spores and very dissimilar pigments. The *Cantharellaceae* are even more sharply separated from *Hygrophoropsis* since their basidia are stichic. The *Leptotaceae* are, in the opinion of the author, probably not true agarics, and if they were, they would under no circumstances be considered as related to *Hygrophoropsis.* Their habit is never clitocyboid, their consistency is never fleshy and bolete like in softness, their margin is never involute, and their pigmentation is different in every regard.

The *Paxillaceae* and the *Gomphidiaceae* are no doubt related, as may be expected of two lamellate families close to the *Boletaceae* and *Strobilomycetaceae.* Their tramal structure has some analogies. But biologically, in spore color and spore size, in chemical characters, and, most important, in clamp connections, they are different. In many ways, the *Gomphidiaceae* are comparable with the *Strobilomycetaceae* while the *Paxillaceae* can be compared with the *Boletaceae.*

Phylogeny. The origin of the *Paxillaceae* is rather difficult to determine. The close affinity with the *Boletaceae, Gyrodontoideae,* would place them rather low in the group of families formerly designated as « *Boletineae* ». It may therefore be allowed to assume the existence of a common ancester of the *Paxillaceae* and the primitive *Boletaceae,* perhaps a fungus similar to *Gastroboletus* Lohwag. Within the *Paxillaceae, Hygrophoropsis* shows most traces of primitive origin but it may also be a simplified form derived from the sect. *Pannoides* (less spore pigment, — less readiness to give color reactions with iron salts and alkali); *Neopaxillus* and *Linderomyces* are both side branches with very peculiar trends of development, the latter possessing a conductive system that is unique among the fungi, and *Neopaxillus* combining « boletoid » characters with echinate, ocher-brown spores which are reminiscent of the *Cortinariaceae.* In the *Paxillaceae,* there is also another trend of interest, one that is developed as much as in the *Rhodophyllaceae:* Some of the genera develop pleurotoid forms which — in contrast to the centrally stipitate forms — are lignicolous. This trend is strong in *Clitopilus* and not quite so strong but undeniable in *Rhodophyllus.* As for the *Paxillaceae,* it is expressed in the section *Pannoides* of *Paxillus,* and in *Hygrophoropsis Tapinia.*

KEY TO THE GENERA

A. Spore print at least « chamois » (Ridgway), or deeper brownish; lamellae more or less anastomosing, at least in some parts of the hymenophore, or with transversal veins of rugose ridges on the sides of the lamellae, or if not anastomosing or rugose at all, producing spores with rough or echinate wall; chemical reagents such as $FeSO_4$, KOH, and NH_4OH usually reacting strongly with the surfaces and the context of the carpophores.

B. Spores completely smooth; lamellae more or less anastomosing; coscinoids either absent or indistinctive. 139. *Paxillus*

B. Spores not smooth; lamellae not much anastomosing, or coscinoids present.

C. Coscinoids present; spores verrucose-rough; ornamentation of type XII. Palaeotropical genus. 140. *Linderomyces*

C. Coscinoids none; spores echinate; ornamentation of type VI Neotropical genus. 141. *Neopaxillus*

A. Spore print almost white (somewhat cream colored in thick layer; individual spores under the microscope often with a slight yellowish reflex); lamellae little or not anastomosing but strongly forked, not venose on the sides; chemical color reactions weak or none; spores always smooth. 138. *Hygrophoropsis*

138. HYGROPHOROPSIS (Schrot. in Cohn) R. Maire apud Martin-Sans

L'Empoisonnement, p. 99. 1921.

Type species : H. aurantiaca (Wulfen ex Fr.) R. Maire.

Syn : *Cantharellus* subgenus *Hygrophoropsis* Schröter apud Cohn, *Krypt.-Fl. Schlesien, Pilze* 1 : 511. 1889.

Merulius S. F. Gray, *Nat. Arr. Brit. Pl.* 1 : 636. 1821 (non Fr.)

Characters : Pileus somewhat tomentose with involute margin when young; spore print pallid; hymenophore lamellate; lamellae decurrent, narrow, arcuate, with somewhat obtuse edges and strongly, usually repeatedly forked; spores subhyaline or with a yellowish reflex, smooth, small to barely medium sized, with thin, simple, non-amyloid walls, subglobose, short-ellipsoid, ellipsoid, ellipsoid-oblong, or cylindric; basidia small and mostly 4 spored, normal in all regards; cystidia absent; hymenophoral trama consisting of a mediostratum or trama proper where the hyphae are distinctly axillarly arranged, subparallel subinterwoven, or subparallel, with often somewhat thickened walls, looser than in the outer layer, the latter — the hymenopodium in our terminology — denser, less regular to rather intermixed, at places subdivergent (near the edge — but this divergence is inconstant and not persistent); the mediostratum continued

above the interlamellar space as in the boletes; the subhymenium little differentiated from the hymenopodium (as in the *Rhodophyllaceae, Gomphidiaceae*, etc.); stipe either central or lateral, or eccentric or absent; context fleshy soft as in the boletes (*Boletus*); chemical reactions with $FeSO_4$, KOH, and NH_4OH not striking as far as color changes are concerned. All hyphae with clamp connections. On the ground, in deep moss, and on wood or sawdust.

Development of the carpophores: Unknown.

Area: One species in temperate regions of Europe, Asia, and North America, almost preferring the boreal part of the Northern Hemisphere, another species in Tropical Florida.

Limits: These were discussed under the limits of the family *Paxillaceae*, p. 626.

State of knowledge: Two species are known in all essential details.

Practical importance: None. *H. aurantiaca* was formerly believed to be poisonous but its edibility is now established. However, this fungus has no economic importance.

SPECIES

H. aurantiaca (Wulfen ex Fr.) R. Maire apud Martin Sans (Cantharellus, Fr.; Merulius, Pers. ex S. F. Gray; Clitocybe, Studer, with var. *nana* Sing.; *H. Tapinia* Sing.

KEY TO THE SPECIES

A. Habit clitocyboid, rarely somewhat pleurotoid; spores 4.8-8 × 2.7-4.8 μ. From the boreal to the subtropical zone . . . . . *H. aurantiaca*

A. Habit pleurotoid; spores 3.3-4.8 × 2.5-3.3 μ. Florida . . . . . *H. Tapinia*

139. PAXILLUS Fr.

Gen. Hymen., p. 8. 1836.

Type species: *P. involutus* (Batsch ex Fr.) Fr.

Syn.: *Rhymovis* Opatowski, *Comm. Bolet.*, *Wiegm. Arch.* **2**: 4. 1836 (proposed for rejection).

Rhymovis Rabenh., *Kryptogamenflora* **1**: 453. 1844.

Tapinia Karst., *Hattsv.*, *Bidr. Finl. Nat. Folk* **32**: xxiii. 1879.

Tapinella Gilbert, *Bolets*, p. 67. 1931.

Plicaturella Murr., *N. Am. Fl.* **9**: 172. 1910.

Paxillopsis Gilbert, *Bolets*, p. 86. 1931 (nom. nud.), non Lange 1939.

Parapaxillus Sing. ad int., *Ann. Mycol.* **40**: 58. 1942.

Characters : As in *Hygrophoropsis* but spore print at least « chamois » (Ridgway) or deeper brownish (e. gr. « oak », or Pl. 14, J 11-12 to K 11 12, Maerz & Paul); spores yellowish to brownish under the microscope, smooth, with moderately thin wall without germ pore or callus; lamellae often anastomosing, especially near the stipe, sometimes venose rugose on the sides, often easily separable from the context of the pileus; hymenophoral trama often consisting of a mediostratum, a diverging lateral stratum and an irregular hymenopodium (e. gr. in *P. involutus*), or else of simpler structure but always diverging; stipe central, eccentric, lateral, or absent; veil present, or more often absent; context sometimes becoming brown; cystidia sometimes present on the sides and edges of the lamellae; basidia normal in every regard; chemical color reactions with $FeSO_4$, KOH, NH_4OH, etc. usually striking. On the ground and on wood.

Development of the carpophores : Unknown in detail.

Area : Cosmopolitan.

Limits : Paxillus is close to two genera : *Hygrophoropsis* and *Gyrodon*. The differences between *Paxillus* and *Gyrodon* have been pointed out in the corresponding paragraph under *Paxillaceae*, p. 625. The differences between *Paxillus* and *Hygrophoropsis* are obvious in the key, p. 628.

State of knowledge : The species of *Paxillus* are well known. They have been monographed by Singer for the state of Florida (*Farlowia* **2** : 537 544. 1946). Six species are recognized. Three of these are completely known including the chemical reactions. Three are known in all essential characters but not the chemical ones.

Practical importance : P. panuoides is an active wood destroyer, and forms carpophores even in the darkness of coal mines, cellars and similar places. In contrast to *Lentinus lepideus,* these carpophores are normally developed. The timber attacked is weakened and destroyed. *P. involutus* is the « babye ookhy » of the Russian farmer who considers it second rate but salts it in large numbers in years when other mushrooms are not available in sufficient quantity.

SPECIES

Sect. 1. **ATROTOMENTOSI** Sing. (1946). Stipe present, vellereous, central or eccentric, rarely lateral naked; spores small (up to 7.5 μ); cystidia none; trama sometimes bright colored (blue, lilac, etc.),

Type species : ***P. atrotomentosus*** (Batsch ex Fr.) Fr.

P. atrotomentosus (Batsch ex Fr.) Fr.; ***P. polychrous*** Sing.

Sect. 2. **PANUOIDES** Sing. (1946). Pileus almost sessile; spores small (up to 6 μ); cystidia none.

Type species : ***P. panuoides*** (Fr. ex Fr.) Fr.

P. panuoides (Fr. ex Fr.) Fr. [P. rudis Berk. & Curt.; P. ligneus Berk. & Curt.; P. acheruntius (Humb. ex) Schroter; P. lamellirugis Quél.; P. ionipus Quél.]; ***P. Curtisii*** Berk. apud Berk. & Curt. (P. corrugatus Atk.).

Sect. 3. **INVOLUTI** Sing. (1946). Pileus centrally, eccentrically, or laterally stipitate; stipe glabrous; veil sometimes present; spores larger than 6 μ; cystidia present.

Type species : ***P. involutus*** (Batsch ex Fr.) Fr.

P. involutus (Batsch ex Fr.) Fr.; also ***P. argentinus*** Speg. (which may be considered the type of another, independent section).

KEY TO SPECIES

A. Spores up to 7.5 μ in length; cystidia none; veil none.
- B. Stipe present, voluminous, tomentose-velleroús.
  - C. Hymenophoral trama lilac, blue in NH_4OH. Eastern Europe. ***P. polychrous***
  - C. Hymenophoral trama not as above. Temperate species. ***P. atrotomentosus***
- B. Stipe present, and then lateral and short, or absent.
  - D. Spores 3.8-6 × 3-4.5 μ; odor none or not remarkable. Widely distributed. ***P. panuoides***
  - D. Spores 3-4 × 1.7-2 μ; odor sometimes persistent, disagreeable. Eastern North America. ***P. Curtisii***

A. Spores, at least their majority, larger than 7.5 μ, or cystidia present, or veil present.
- E. Veil none. Eastern and Western Hemisphere from the subarctic to subantarctic region. ***P. involutus***
- E. Veil present. Province of Buenos Aires (Argentina). ***P. argentinus***

140. LINDEROMYCES Sing.

Farlowia **3** : 157. 1947.

Type species : ***L. lateritius*** (Petch) Sing.

Characters : Differing from *Paxillus* in the presence of coscinoids (Pl. XVIII, 6), and coscinocystidia, in warty rough spores and in bright colors (when fresh). On the ground.

Development of the carpophores : Unknown.

Area: Tropical Asia (Ceylon).

Limits: This genus is well separated from all other agarics by the coscinoids. Besides, it differs from *Paxillus* in the rough spores and the presence of red pigment. The genus most closely related to *Linderomyces*, is, nevertheless, *Paxillus*. The habit of the carpophores is similar to that of *Paxillus involutus*, and the type species of *Linderomyces* stains purple brown which is reminiscent of *Paxillus involutus* which stains brown.

State of knowledge: Only one species is known.

Practical importance: None.

SPECIES

L. lateritius (Petch) Sing. (Paxillus, Petch).

141. NEOPAXILLUS Sing.

Mycologia 40: 262. 1948.

Type species: N. echinosporus Sing. (= *N. echinospermus*).

Characters: Habit clitocyboid omphalioid, reminiscent of a small form of *Phylloporus rhodoxanthus*; pileus depressed in the center; cuticle a trichodermium palisade consisting of brown (by membrana-pigment) hyphal chains which are erect and parallel with each other, or subparallel, the terminal member broadly clavate, 17-42 × 5-17 μ in the type species; hymenophore lamellate; lamellae rather distant, occasionally anastomosing by veins, dull rusty brownish in dried specimens, deeply decurrent, and anastomosing on the stipe; hymenophoral trama in youth bilateral, later consisting of a mediostratum of subparallel, strictly axillarly arranged hyphae; this is flanked by the interlaced intermixed, broad hymenopodium whose hyphae are densely packed and only at places tending to be subparallel, accompanying the subhymenium around the interlamellar spaces; the latter is a thin layer, well developed but not very sharply separated from the hymenopodium, consisting of short-cylindric to subisodiametric cells; basidia 4 spored, some 2 spored, clavate; cystidia none in the type, but some sterile cells (cystidioles) often seen on the edge and near it; spore print near « oak » (Maerz & Paul); spores under the microscope with a rusty brown ornamentation on paler ground, the

at maturity beset with cylindric spines of 0.8-1.0 μ (in the type species) whose lower portion may be somewhat inserted in the wall proper, wall moderately thick, not interrupted by a germ pore or a callus, size of the spores medium (8.5-10 μ in diameter), shape globose; stipe central or almost so, without a veil; mycelium whitish, sparse. All hyphae with clamp connections. $FeSO_4$ olive on pileus; deeper colored with NH_4OH and KOH; phenol causing a reddish chocolate discoloration. On the ground.

Development of the carpophores : Unknown.

Area : Brazil, Paraguay, Argentina (northern part and south to Cordoba).

Limits : This genus seems to connect the *Paxillaceae* with the *Cortinariaceae.* The structure of the trama, the habit of the carpophores, the combination of rather distant and at the same time distinctly decurrent lamellae, all this is in favor of the *Paxillaceae.* And the spores, even though they undoubtedly remind one of the spores of the *Cortinariaceae* in color and ornamentation, are not quite identical with the spores of any known genus or species in the *Cortinariaceae.* None of the *Cortinarii* has echinate spores with cylindric spines, especially when the spores are globose, and the lamellae decurrent. Besides, all *Cortinarii* have a cortina. The structure of the cuticle also reminds one more of the *Boletineae* than of the true agarics. The genus may be determined as *Tubaria* if one follows the older keys, and there is a danger that these two genera might be confused as they have been confused by Rick who collected the type as a *Tubaria.* However, *Tubaria* never has truly echinate spores and even if they appear to be finely echinulate, they are not globose. It is not quite impossible that there is an actual affinity between *Neopaxillus* and *Tubaria,* section *Thermophila,* but even so, they are not congeneric, nor can they be put into the same family.

State of knowledge : The most important data on the one species known, including those on the chemical characters, have been obtained by the author.

Practical importance : None.

SPECIES

N. echinospermus (Speg.) Sing. (Naucoria, Speg.; Neopaxillus echi-

GOMPHIDIACEAE R. Maire

Publ. Junta Cienc. Nat., Barcelona, p. 43. 1933.

Type genus : Gomphidius Fr.

Characters : Habit clitocyboid; pileus glabrous or tomentose or farinaceous-mealy, viscid to glutinous or more rarely dry, small to rather large; hymenophore lamellate, consisting of rather thick, decidedly decurrent gills with frequently obtuse edges (less so in *Gomphidius*, subgenus *Chroogomphus*), waxy subgelatinous to tender-fleshy in consistency, with rather thick trama, subdistant to distant, more rarely subclose, more or less arcuate, gray to fuliginous when mature but assuming a rusty fuliginous tinge when kept in the herbarium for a long time; spore print from « bone brown » (Ridgway) or « Buffalo » (Maerz & Paul) to nearly black, usually assuming a rusty-brown color when preserved in the herbarium for some time; spores (Pl. XXVII, 3-4) always elongate, fusoid to subcylindric, often with distinct suprahilar depression, without a distinct germ pore or callus in most cases, smooth, melleous or gray under the microscope; basidia (Pl. XXVII, 2, 6) normal and usually 4 spored, rather elongate when forming the spores; cystidia (Pl. XXVII, 1, 7) large and projecting, usually distinctly incrusted by a resinous matter of chestnut or fulvous color, sometimes with very thick walls (Pl. XXVII, 7), numerous to (rarely) scattered in old specimens; hymenophoral trama typically bilateral in some species, the mediostratum consisting of parallel to subparallel hyphae, forming a very thin and often evanescent layer, the lateral stratum initially diverging, often subevanescent in adult specimens; hymenopodium very broad, consisting of strongly interwoven and entirely irregular elements which are not clearly separated from the subhymenium in some species while in others the latter is well differentiated; subhymenium variable in structure; stipe versiform, equal or swollen, etc., in most species and specimens with a discolored (bright yellow, rarely reddish to pink) base both inside and on the surface; veil present or absent, more often present, and then either entirely glutinous, or tender and fibrillose, or mealy and consisting of a loose pseudoparenchyma, sometimes forming an annulus; glandulae present on the surface of the stipe of only one species; all hyphae without clamp connections. On earth, forming mycorrhiza with conifers.

Limits : This small family is very sharply separated from all other families.

Phylogeny : The *Gomphidiaceae* are biologically so similar to *Suillus*, and some characters are quite similar to those of the *Strobilomycetaceae*, especially *Porphyrellus*, one is led to believe that these two families and the *Gomphidiaceae* must have a common ancestor. Whatever the phylogeny of the *Gomphidiaceae* will turn out to be in detail, this family is obviously closely related to and part of the group of families that was formerly combined into the suborder *Boletineae*.

142. CYSTOGOMPHUS Sing.

Ann. Mycol. **40** : 51. 1942.

Type species : C. Humblotii Sing.

Characters : As in the family, but veil consisting of spherocysts. On the ground in coniferous plantations.

Development of the carpophores : Not studied in detail.

Area : Unknown. The type species is known only from coniferous plantations near Paris. The conifers were of foreign origin.

Limits : These are clearly recognizable in the key.

State of knowledge : This genus contains thus far only one species which is perfectly well known in all essential characters.

Practical importance : Probably a mycorrhizal fungus, and therefore potentially important in forestry.

SPECIES

C. Humblotii Sing.

143. GOMPHIDIUS Fr.

Gen. Hymen., p. 8 1836.

Type species : G. glutinosus (Schaeff. ex Fr.) Fr.

Characters : Those of the family, but veil never consisting of spherocysts, in fact all the cortical layers deprived of spherocysts. On the ground in coniferous woods.

Development of the carpophores : Known in detail (Reynders 1933). It is, in contrast to *Suillus*, not pseudoangiocarpous but hemiangio-

Area : Temperate zone of the northern hemisphere, probably all through the area of coniferous woods, penetrating the subtropics and the mountain districts of the tropics wherever there are stands of conifers *(Pinus)*.

Limits : These are evident from the keys. *Gomphidius* is an exceptionally well delimited and almost isolated genus.

State of knowledge : The 16 species are well known.

Practical importance : The *Gomphidii* are specialized mycorrhizal fungi, as much or more so than the *Suilli*, some of them growing in close association with certain species of the *Suilloideae* (*Boletaceae*). As such they are likely to play a major practical rôle in foresty, especially in reforestation projects. All *Gomphidii* are edible.

SPECIES

Subgenus I. **Chroogomphus** Sing. (1948). Context colored; veil present, consisting of parallel, strongly incrusted hyphae (Pl. XXVII, 5); subhymenium dense, filamentous intermixed and irregular.

Type species : G. rutilus (Schaeff. ex Fr.) Lundell & Nannfeldt.

Sect. 1. FLOCCIGOMPHUS Imai (1938). Pileus dry to subviscid, not shining when dry, more or less tomentose or fibrillose.

Type species : G. tomentosus Murr.

G. tomentosus Murr.; *G. leptocystis* Sing.; *G. sibiricus* Sing.; *G. helveticus* Sing. Possibly also *G. viscidus* var. *tatrensis* Pilat.

Sect. 2. VISCOGOMPHUS Imai (1938). Pileus viscid, shining when dry in most of the individual carpophores (but not always, depending on the manner of preparation), not tomentose and not fibrillose when mature.

Type species : G. rutilus (Schaeff. ex Fr.) Lundell & Nannfeldt.

G. vinicolor Peck with ssp. *typicus* (Northeastern part of North America); ssp. *jamaicensis* (Murr.) Sing. (Southern part of North America and West Indies); ssp. *californicus* Sing. (West Coast of North America); *G. ochraceus* Kauffm.; *G. rutilus* (Schaeff. ex Fr.) Lundell & Nannfeldt [G. viscidus (L. ex) Fr.; G. testaceus (Fr.) Britz.], ssp. *typicus* (Europe and northern part of North America) and ssp. *alabamensis* (Earle ex) Sing.

Subgenus II. **Laricogomphus** Sing. (1948). Context more or less reddening when bruised; veil almost none; subhymenium filamentous, moderately dense; mediostratum moderately distinct in mature

specimens; dermatocystidia of the stipe fasciculate, mostly forming distinct small glands. Mycorrhiza with *Larix*.

Type species: *G. maculatus* (Scop. ex Fr.) Fr.

G. maculatus (Scop. ex Fr.) Fr. (G. gracilis Berk. & Br.); *G. flavipes* Peck.

Subgenus III. **Myxogomphus** Sing. (1948). Context of the pileus white or somewhat pinkish, or turning pink when bruised; veil well developed, consisting of hyphae which are not incrusted, and not quite strictly parallel with each other but rather subparallel-subinterwoven; subhymenium filamentous to subfilamentous-subcellular (chains of small globules), only moderately dense; mediostratum moderately distinct in mature specimens; dermatocystidia of the stipe scattered and not fasciculate, without small glands; mycorrhiza with various conifers but never with *Larix*.

Type species: *G. glutinosus* (Schaeff. ex Fr.) Fr.

Sect. 1. **MACROSPORUS** Sing. (1948). Mature spores longer than 14 µ.

Type species: As in subgenus.

G. septentrionalis Sing.; *G. nigricans* Peck; *G. Smithii* Sing.; *G. roseus* (Fr.) Karst.; *G. subroseus* Kauffm.; *G. glutinosus* (Schaeff. ex Fr.) Fr.

Sect. 2. **MICROSPORUS** Sing. (1948). Mature spores 14 µ long or shorter.

Type species: *G. oregonensis* Peck.

G. oregonensis Peck.

KEY TO THE SPECIES

A. Context of the pileus ochraceous to orange (though at times in young specimens rather pallid colored), more rarely salmon to pink; veil constantly present, consisting of strictly parallel, pigment-incrusted hyphae, macroscopically never entirely glutinous, never hyaline; subhymenium filamentous-intermixed and dense to very dense; mediostratum rudimentary in young specimens, indiscernible in old ones.

B. Pileus dry to subviscid in wet weather, more or less tomentose or fibrillose.

C. Base of the stipe with deep orange context. Under *Pinus sibirica* in the Altai Mts. *G. sibiricus*

C. Base of the stipe yellow, not deep orange. Not under *Pinus sibirica* and not in Central Asia

D. Pileus appressed-fibrillose or with appressed tomentum, and becoming flocculose-subsquarrulose in old specimens, especially on the disc; color of the freshly dried pileus purple; cystidia

thin walled (walls up to 1 µ thick), collapsing in poorly dried or very old material and then not readily demonstrated. From British Columbia to Oregon and east to Idaho. *G. leptocystis*

D. Pileus tomentose, the tomentum eventually disintegrating, forming appressed squamules; color of freshly dried pileus some shade of pink with the tomentum more olive-ochraceous; cystidia thick-walled (walls 1-4 µ thick) or thin walled, never collapsing, numerous in old specimens.

E. From Japan to the American West Coast. Cystidia thick-walled. *G. tomentosus*

E. Europe. Cystidia thin-walled. *G. helveticus*

B. Pileus viscid in wet weather.

F. Mycelial tomentum pink or pallid-salmoneous.

G. Cystidia thick-walled in their middle portion or near their base. North and Central America. *G. vinicolor*

G. Cystidia thin-walled throughout. North America, more common in the West. *G. ochraceus*

F. Mycelial tomentum Isabella color, or melleous, or light to bright yellow; cystidia thin walled throughout. Europe, parts of Asia and Africa, all over North America. *G. rutilus*

A. Context of the pileus white, more rarely partly more or less salmon color, or becoming so on exposure; veil absent, or consisting of subparallel subinterwoven, thin hyphae which are not incrusted by pigment, macroscopically hyaline to white, and often partly or entirely glutinous, sometimes gradually blackening in age; subhymenium filamentous-cellular to filamentous, moderately dense; mediostratum of young specimens distinct, less distinct in older ones.

H. Veil visible only in the primordium, fugacious and not leaving traces in adult specimens; dermatocystidia of the stipe fasciculate and the fascicles often forming granulae; mycelium (of *G. maculatus*) connected with *Larix* mycorrhiza.

I. Pileus « vinaceous pink » (Ridgway) when young; spores [illegible] × 7.5-8.2 µ. New York to Michigan, U. S. A. *G. flavipes*

I. Pileus more brownish than « vinaceous pink » or whitish when young; spores 18-25 × 7-9 µ. Circumpolar with *Larix* ssp.
G. maculatus

H. Veil covering the lamellae of young carpophores and leaving more or less distinct traces in old specimens; dermatocystidia of the stipe not fasciculate; mycelium in nature not connected with larch but rather forming mycorrhiza with a variety of other conifers (*Pinus*, *Picea*, *Tsuga*, *Pseudotsuga*, *Abies*).

J. Spores mostly larger than 14 µ.

K. Veil essentially fibrillose, or partly fibrillose and partly glutinous, in the latter case the glutinous portion manifesting itself in the mature specimen by forming 1-3 slimy belts at the apex of the stipe but not forming a wide glutinous sheath; context salmon color or somewhat pinkish in fresh and dried material

except for the lower portion of the stipe which is deep brilliant yellow or bright yellow, rarely pink-red.

L. European species with *Pinus silvestris*. *G. roseus*

L. American species whit *Picea* and *Abies*, from the Maritime Provinces in Canada south to Maine. *G. septentrionalis*

K. Not combining these characters.

M. Species occurring in Eastern North America with concolorous base (white), forming mycorrhiza with Eastern White pine (*Pinus strobus*). *G. nigricans*

M. Western American species, or species with very strongly and brightly yellow base.

N. Cystidia of recently dried specimens, if treated with formalin, and afterwards mounted in KOH, frequently pinkish, or at least incrustations of the elements of the hymenium partly or entirely deep pink to purplish red, subhypodermal zone and sometimes also the base of the stipe turning pinkish to red on injury; pileus « purplish vinaceous » to « pale grayish vinaceous » (Ridgway), or colored in similar « cold » pallid hues, pallescent in age. *G. Smithii*

N. Cystidia and other hymenial elements not reacting in the manner described above; context not changing to pink or red in any part, or at least not becoming so by autoxidation when injured; pileus either more salmoneous-testaceous or more distinctly livid brown, not or not strongly and consistently pallescent.

O. Pileus some combination of pink, carpophore in average medium sized; spores 12-22 × 4.8-6.8 μ, mostly 14.2-18.5 × 5.8-6.8 μ — when taken from a print; mycelium most frequently associated with *Abies* or *Pseudotsuga*. Western species (North America). *G. subroseus*

O. Pileus livid brown, never pink; the average carpophores rather tall and stout; spores 15-24 × 4-7.5 μ, mostly 15.3-20 × 5.2-6.2 μ, i. e. slightly longer than in *G. subroseus*, and slightly narrower in prints taken from American specimens. Circumpolar species of the Northern hemisphere occurring under *Abies* and *Pseudotsuga* but also under *Pinus* and very frequently under *Picea*. *G. glutinosus*

J. Spores smaller than 14 μ. Western North America. *G. oregonensis*

DOUBTFUL GENERA

Melanomphalia Christiansen, *Friesia* 1: 288. 1936. « Pileus umbilicate; veil none; lamellae broadly adnate-decurrent; spores smooth,

olive gray in mass, or brownish olive-black; cystidia none. » Christiansen. The type species is *M. nigrescens* Christiansen. This species is described as squamose-tomentose, hygrophanous, olive brown, with pilose-fibrillose margin; lamellae distant, olive gray-brown with blackish edge; stipe fibrillose-to woolly-tomentose; context brown; spores oblong-lemon shaped 9,6-12.5 × 6-6.8 μ. It is said to grow on the earth among grasses in Denmark. The type specimen is preserved at the Landbohojskolens Plantepatologiske Herbarium in København. The author has not seen this material. It appears uncertain that this should actually be a new genus of the *Gomphidiaceae* (*Gomphidieae* as proposed by Lange). One is rather tempted to consider it as closer to the *Strophariaceae* or *Coprinaceae*, but any further comment is impossible unless the type furnishes data on the (1) spores: whether there is a germ pore or not, (2) cuticle: whether there is a trichodermium or an epithelium on the pileus, (3) on the hyphae: whether there are clamp connections, (4) on the hymenium: whether cystidia are actually absent, even on the edge of the lamellae, (5) on the chemical reactions: whether strong reactions are obtainable with H_2SO_4, i. e. whether or not the spores are bleached in a concentrated solution of that reagent (6) on the hymenophoral trama: whether the structure is regular or bilateral.

Gymnogomphus Fayod, *Prodrome, Ann. Sc. Nat. Bot.* VII. 9: 385. 1889. « Carpophores naked, with central or subeccentric stipe, probably gymnocarpous, homomorphous » (i. e. homoiomerous); « lamellae arcuate, broad, decurrent; hymenophoral trama intermixed; cystidia cylindric, naked; spores large, fusiform, with hilar depression, as those of *Gomphidius*, but pale brown. On the earth. » This genus is hyponymous since no type species is indicated. It is based on two species from Japan (collection Döderlein) which were never published by Fayod as far as the author knows. Various guesses as to the taxonomic position of this genus are permissable. One possibility was pointed out by the author (1946) who suggested that *Gymnogomphus* might be a late stage of certain *Gomphidii*. It is also possible that Fayod's *Gymnogomphus* is nothing but *Phylloporus*, also in an advanced stage (because of the intermixed trama). The generic name *Gymnogomphus* is invalid, and it does not matter what species it was meant to describe.

BOLETACEAE R. Maire

Bull. Soc. Bot. Fr., tab., 1901 (nud. non.); *Recherches*, p. 166. 1902 both as Boletacées); Lotsy, *Vortraege*, p. 717. 1907.

Type genus : Boletus Dill. ex Fr. sensu Gilbert.

Syn. : *Leucosporelleae* Gilbert, *Bolets*, p. 100. 1931
Gyreae Gilbert, *Bolets*, p. 102. 1931.

Characters : Pileus scaly, fibrillose, mealy, tomentose, granulose, velutinous, or glabrous, often becoming tesselate-rimose, viscid or dry, small to large, the margin sometimes projecting; hymenophore tubulose, rarely lamellate (in *Phylloporus*); tubes short to long, decurrent or adnate to depressed around the stipe, or free; pores very small or closed when quite young to very wide and open from the beginning, sometimes lamellately arranged (« boletinoid »), and then not so easily separated from the context of the pileus, usually very easily separable from the context, in one genus (*Fecchinus*) all the single tubes free from each other, discolorous, or more frequently concolorous with the pores, whitish to sordid, or whitish to yellowish, or yellow to golden yellow, more rarely orange to red, the pores sometimes orange to red or reddish brown, at last often olivaceous or yellowish brown, sometimes becoming dirty livid or blue to green on pressure; spore print olivaceous to deep olivaceous, cinnamon, or fawn color to vinaceous pink, or ochraceous, or lemon yellow; spores usually not very richly colored under the microscope even when quite mature (except in *Xanthoconium* where they are bright golden), most frequently pale melleous or brownish melleous, or pale yellowish, even hyaline, always smooth with homogeneous wall, which rarely reaches as much as 1 µ in diameter, their length rarely over 20 µ, usually well below 20 µ, without germ pore and callus, globose, subglobose, short ellipsoid to ovoid, fusoid subcylindric, fusoid ellipsoid, ovoid fusoid (clavate), or cylindric; basidia and cystidia usually comparatively small, more rarely large; hymenophoral trama more or less bilateral in youth, in some genera with less striking bilaterality (*Phyllophorus* subtype of the bilateral type); interlaced hymenopodium absent; hyphae with or without clamp connections; stipe cylindric, attenuate or thickened toward the base, or ventricose to bulbous, smooth and glabrous or ornamented with glandulae, with furfuraceous floccons, with scabrous squamules, or with reticulate lines, solid to hollow; veil often present, and then

membranous, or membranous floccose, or glutinous, or pulverulent (and then mostly yellow), either fugacious or persistent as an annulus on the stipe. On earth, more rarely on decayed wood in wooded areas, one species (*Xerocomus parasiticus*) on living carpophores of *Scleroderma* (*Gastromycetes*), the majority symbiotic with forest trees, forming mycorrhiza.

Limits: The delimitation of the *Boletaceae* from the *Paxillaceae* and the *Strobilomycetaceae* is discussed under these families.

Phylogeny : The author believes that the subfamily *Gyrodontoideae* is the lowest group among the *Boletaceae* and probably goes directly back to the ancestral form which is envisaged as being similar to *Gastroboletus*. A slightly higher development can be noticed among the *Suilloideae* which are mostly connected with conifer-mycorrhiza, and finally, the highest level is reached with such genera as *Tylopilus* and especially *Leccinum* (the latter forming mycorrhiza almost exclusively with *Salicales* and *Fagales*) and perhaps also such specialized groups as *Boletochaete* of the African and Asiatic tropics.

KEY TO THE SUBFAMILIES

A. Clamp connections constantly present except in occasional parthenogenetic forms, and easily observed on at least a fair percentage of the septa; tubes not boletinoid; spores always rather short, i. e. not more than twice as long as broad. *Gyrodontoideae*, p. 643

A. Clamp connections either not constant in a genus (and then the tubes boletinoid and the spores elongate), or very sparse (not more than 10 clamps to 100 septa), or persistently lacking.

B. Hymenophore boletinoid, or entirely red to pink (not merely the pores discolored), or stipe with glandulae, all except one species (*Suillus tabinus*) forming mycorrhiza with conifers exclusively *Suilloideae*, p. 648

B. Hymenophore not boletinoid, and not pink or red inside, and stipe not glandulose; mycorrhiza with conifers or with other trees or shrubs, or else mycorrhiza not selective, or perhaps mycorrhiza not always formed.

C. Pileus appressedly squamulose or strongly viscid; NH_4OH reacting more or less pink or reddish-lilac or green with some parts of the carpophore; stipe equal; spores usually smaller than 10 μ and rather pale melleous, elongate, i. e. more than twice as long as broad; cystidia rather large and incrusted; hymenophoral trama of the *Boletus*-type (lateral stratum strongly divergent and hyaline, very loosely arranged); hymenophore adnate; mycelium forming mycorrhiza exclusively with conifers. (see *Suilloideae*, p. 648)

C. Not combining all these characters.

D. Lateral stratum of the hymenophoral trama slightly divergent, only little paler (if at all) than the mediostratum, and its walls

touching each other, often becoming somewhat irregular in age (*Phylloporus* type of trama); hymenophore made up of lamellae or tubes; spore print always olive brown or olive

Xerocomoideae, p. 663

D. Hymenophoral trama of the *Boletus*-type, hymenophore always made up of tubes; spore print olive brown, olive, or some other color. *Boletoideae*, p. 669

Subfamily **Gyrodontoideae** Sing.

Farlowia **2**: 230. 1945.

Type genus: Gyrodon Opat.

Characters: Hyphae with clamp connections; spores ellipsoid or globose, brownish or yellow.

Note: The combination of the *Gyroporus* group (tribus *Leucosporelleae* (Gilbert) Sing. 1936; family *Leucosporelleae* Gilbert) and the *Gyrodon* group (tribus *Gyrodonteae* Sing. 1936; family *Gyreae* Gilbert) into a single subfamily is the result of recent studies on tropical boletes. The genus *Phaeogyroporus* represents a perfect connecting link between the two groups.

KEY TO THE GENERA

A. Hymenophore depressed or subfree around the apex of the stipe, not arcuate-decurrent.

B. Spore print yellow. 144. *Gyroporus*

B. Spore print olive brown. 145. *Phaeocyroprous*

A. Hymenophore more or less arcuate-decurrent.

C. Veil present. 146. *Paragyrodon*

C. Veil none. 147. *Gyrodon*

144. **GYROPORUS** Quél.

Enchiridion, p. 161. 1886, *em.* Pat. (1900).

Type species: G. cyanescens (Bull. ex Fr.) Quél.

Syn.: Suillus Karst., *Bidr. Finl. Nat. Folk* **37**: v. 1882, non S. F. Gray (1821).
Coelopus Bat., *Boleti*, p. 12. 1908.
Leucobolites G. Beck, *Zeitschr. Pilzk.* **2**: 146. 1923.
Leucoconius G. Beck, *Zeitschr. Pilzk.* **2**: 146. 1923.

Characters: Pileus non viscid, glabrous to coarsely fibrous-subsquamose; cuticle made up of repent to ascendant elongate but

terminal members often cystidioid and in palisade (Pl. XXV, 1) hymenophore tubulose with concolorous small to more often medium-sized to large pores, depressed around the stipe, rather long, white, pink, or pallid stramineous; spore print yellow (« Colonial buff », « amber yellow », « citron yellow » Ridgway); spores (Pl. XXV, 4) stramineous-subhyaline to yellowish, ellipsoid, rarely more elongate than twice as long as broad, of medium size but rather variable in this regard ; cystidia present in the tubes and on the pores (Pl. XXV, 2) ; hymenophoral trama bilateral, of the *Boletus* type ; stipe hollow or solid, its surface glabrous or fibrous, or subfurfuraceous, not reticulate, without glandulae, without veil, without pseudosclerotium ; context white or whitish, unchanging or becoming blue on injury ; hyphae (except for rare parthenogenetic aberrations) constantly with clamp connections ; the usual inorganic reagents causing little or no color reactions ; said to contain no boletol. On the ground under conifers and under frondose trees, possibly occasionally forming mycorrhiza but sometimes fruiting without mycorrhizal connections, often in open places rather far away from larger trees.

Development of the carpophores : Unknown.

Area : Temperate and tropical regions, widely scattered.

Limits : They are obvious in the key. The parthenogenetic forms that occasionally occur have no clamp connections ; they would key out with the *Boletoideae*, and differ from the latter subfamily in the color of the spore print except for the genus *Xanthoconium* where the spores are golden under the microscope and cylindric rod shaped.

State of knowledge : Out of seven species belonging to *Gyroporus*, six are completely known.

Practical importance : All species are edible and highly estimated by mycophagists.

SPECIES

G. subalbellus Murr. (Suillus, Sacc. & Trotter; G. roseialbus Murr.); *G. umbrinisquamosus* Murr. ; *G. cyanescens* (Bull. ex Fr.) Quél. (Boletus, Fr. ; Suillus, Poiret in Lam. ex Karst.) ; *G. purpurinus* (Snell) Sing. ; *G. castaneus* (Bull. ex Fr.) Quél. (Boletus, Fr. ; Suillus, Poiret in Lam. ex Karst.) ; *G. atroviolaceus* (Hoehnel) Gilbert (Suillus, Hoehn.) ; perhaps also *G. Earlei* Murr.

KEY TO THE SPECIES

See the key published in *Farlowia* **2**: 231. 1944 which takes into account all species as far as known to Singer.

145. **PHAEOGYROPORUS** Sing.

Mycologia **36**: 360. 1944.

Type species: P. Braunii (Bres.) Sing.

Characters: Hymenophore adnexed to depressed, tubulose, pores minute to medium sized; spore print « Isabella color » to « light brownish olive » (Ridgway); spores short-ellipsoid; cystidia present in the tubes and on the pores, normally developed; trama of the hymenophore bilateral; hyphae with clamp connections. On the ground, but sometimes forming cryptas around the roots of trees in a loose mycorrhizal relationship.

Development of the carpophores: Unknown.

Area: Tropical Africa and also in South America from Brazil south to Central Argentina.

Limits: Clearly separated from *Gyrodon* by the habit and from *Gyroporus* by the color of the spore print.

State of knowledge: Both species now known have been studied in a rather complete way as far as their essential characters are concerned.

Practical importance: P. tropicus has been shown to form a mycelium crust around the roots of species of *Citrus* in Brazil covering colonies of *Pseudococcus comstocki* which attack the roots of these plants after they have been carried there by the ants (*Solenopsis saevissima* var. *moelleri*); these mycelial crusts are called criptas by the Brazilian writers, and the author has adopted the term cryptas for English usage. The *Pseudococcus* living in symbiosis with the fungus is thought to be the immediate reason for the subsequent dying of the trees affected, but the action of an endotrophic mycorrhizal fungus weakens the plant sufficiently, before the attack of the *Pseudococcus* takes place. This extremely complicated and interesting cooperation of fungi and animals in symbiosis, epibiosis and parasitism has been described, illustrated, and discussed by Gonçalves and Milanez (*Rodriguesia* 4: 179-263. 1940). The combination of basidiomycetous cryptas and *Pseudococcus* is, by the way, strikingly

analogous in the disease called platyriosis of coffee where the fungous cause is now known to be *Diacanthodes philippinensis*.

SPECIES

P. Braunii (Bres.) Sing. (Boletus, Bres.); *P. tropicus* (Rick apud. Rehm & Rick) Sing. (Boletus, Rick apud Rehm & Rick; Boletus Bruchii Speg.).

146. **PARAGYRODON** (Sing.) Sing.

Ann. Mycol. **40**: 23. 1942.

Type species: *P. sphaerosporus* (Peck) Sing.

Syn.: *Gyrodon* subgenus *Paragyrodon* Sing. *Rev. Mycol.* **5**: 7. 1940.

Characters: Hymenophore decurrent; spore print olive brown; spores subglobose; cystidia conspicuous; stipe with a volva-like annulus which is viscid, white and membranous; hyphae with clamp connections. On the ground, near trees with which it appears to form mycorrhiza.

Development of the carpophores: Unknown; either hemiangiocarpous or pseudoangiocarpous, more probably the former because of the « general » veil.

Area: North America (Iowa, Michigan, Wisconsin, Minnesota).

Limits: The distinct cystidia and the distinct membranous veil in connection with the subglobose spores are enough characters in close correlation to separate this genus from any other boletaceous genus including *Gyrodon*, which is closest.

State of knowledge: The only species known has been studied satisfactorily as far as the essential characters are concerned.

Practical importance: Unknown.

SPECIES

P. sphaerosporus (Peck) Sing. (Boletus, Peck; Ixocomus, Gilbert; Gyrodon, Sing.).

147. GYRODON Opat.

Comm. Hist.-nat. fam. Fung. Bolet., *Wiegmann's Archiv* **2** : 5. 1836.

Type species : *G. sistotremoides* (Fr.) Opat. [111].

Syn. : *Uloporus* Quél., *Enchir.*, p. 162. 1886.
Campbellia Cooke & Massee, *Grevillea* **18** : 87. 1890, non Wight (1850)
Rodwaya Sydow, Hedwigia **40** : (2). 1901
Boletinellus Murr., *Mycologia* **1** : 9. 1909

Characters : Pileus not quite glabrous, inclining to become viscid in wet weather; hymenophore consisting of irregularly arranged (gyrose) or boletinoid tubes or honey-combs, arcuate decurrent; spore print brown to olive brown; stipe not reticulate, not hollow, not glandulose, without a veil, without a pseudosclerotium, not forming cryptas; context either changing color or unchanging on exposure; spores short-ellipsoid to subreniform phaseoliform (but very short), smooth, brownish; cystidia not differentiated except as cheilocystidia on the pores, and even these very inconspicuous; hyphae with clamp connections. On wood or on the ground in woods, often forming mycorrhiza with trees such as *Alnus, Fraxinus*.

Development of the carpophores : Gymnocarpous in *G. lividus*.

Area : Almost cosmopolitan.

Limits : These are obvious from the key, p. 643, and need no further explanation.

State of knowledge : Most of the species are reasonably well known. The author admits now five species. Some more are posibly congeneric but incompletely known.

Practical importance : Some species are edible but they are not popular as food. Some have a potential significance as mycorrhizal fungi in forestry.

SPECIES

G. intermedius (Pat.) Sing. (Phylloporus, Pat.; Boletus, Sacc.; Boletinellus, Gilbert); *G. proximus* Sing.; *G. Rompelii* (Pat. & Rick) Sing. (Phylloporus, Pat. & Rick); *G. merulioides* (Schw.) Sing. (Daedalea, Schw.; Boletinellus, Murr.; Paxillus porosus Berk. in Lea;

[111] As for a discussion of the validity of this genus, and the interpretation of its lectotype, see *Farlowia* **2** : 243. 1945, and the author's type studies on *Boletus*

Boletinus, Peck); *G. lividus* (Bull. ex Fr.) Sacc. [Boletus, Fr.; Uloporus, Quél.; Gyrodon sistotremoides (Fr.) Opat.; Boletus rubescens Trog]; possibly also *G. purpureus* (Berk) Sing. (Favolus, Berk; Boletinellus, Gilbert); certainly *G. africanus* (Cooke & Mass.) Sing. (Campbellia, Cke & Mass.) but macrospically poorly described.

KEY TO THE SPECIES

The species are all keyed out in Singer, *Farlowia* 2: 244. 1945.

Subfamily **Suilloideae** Sing.

Farlowia **2**: 230. 1945.

Type genus: *Suillus* Micheli ex S. F. Gray.

Characters: Pileus glutinous or viscid, or rarely subviscid when wet, or else non-viscid but then with boletinoid hymenophore (in the species with viscid pileus, the hymenophore is either boletinoid or non boletinoid); stipe with glandulae, or non glandulose, with a glutinous or a fibrillose-membranous veil, or without veil (veil never pulverulent and bright yellow at the same time); stipe usually more or less equal, without distinct pseudosclerotium, solid or hollow; hymenophore either completely orange red, deep dusky red, or pink throughout (not merely at the pores), or else some other color but then always forming mycorrhiza with conifers; hyphae with clamp connections or with clampless septa.

Note: The genera *Psiloboletinus*, *Boletinus*, and *Suillus* have very decidedly a close and natural affinity notwithstanding the difficulty one experiences in briefly outlining the characters they have in common. When working on the taxonomy of these fungi in the herbarium, or when observing their mycorrhizal relationships in the field, one cannot fail to notice that there is a much closer affinity between all these genera than between any one of them and any other boletaceous genus.

KEY TO THE GENERA

A. Veil none.

B. Stipe somewhat hollow; hymenophore lamellately arranged near the very margin, more so than near the stipe; pileus not viscid. 148. *Psiloboletinus*

B. Stipe solid, hymenophore not lamellately arranged at the margin or at least not more so than near the stipe; pileus viscid. 150. *Suillus*

A. Veil present, at least in young specimens of a majority of a population

C. Stipe without glandulae ; pileus not viscid, or rarely becoming viscid at maturity, starting from the margin ; surface of the pileus fibrillose, or scaly or floccose (this covering may be the outer layer of the veil when continuing beyond the margin of the pileus in young specimens), hymenophore in most species very strongly boletinoid, never composed of fine pores with a diameter of less than 0 5 mm ; clamp connections present in several species ; stipe hollow in several species. 149. *Boletinus*

C. Stipe with or without glandulae ; pileus viscid on the disc of young specimens, surface of the pileus either glabrous or, if not glabrous, the fibrils are detersible or easily washed off ; hymenophore boletinoid or consisting of tubes with fine pores ; clamp connections absent ; stipe solid. 150. *Suillus*

148. PSILOBOLETINUS Sing.

Farlowia **2** : 250. 1945.

Type species : *P. lariceti* (Sing.) Sing.

Characters : Generally those of the genus *Boletinus,* but without the slightest trace of a veil in mature specimens, and with a hymenophore that becomes more lamella-like at the very margin, not so at the stipe. On the ground in Laricetum.

Development of the carpophores : Unknown.

Area : Central Asia (Altai).

Limits : The limits are obvious.

State of knowledge : Only one species is known.

Practical importance : This seems to be one of the mycorrhizal fungi of the Siberian larch. Its edibility has not been tested. Its practical importance is merely potential.

SPECIES

P. lariceti (Sing.) Sing. (Phylloporus, Sing. 1938).

149. BOLETINUS Kalchbr.

Bot. Zeitschr. **25** : 182. 1867.

Type species : *Boletinus cavipes* (Opat.) Kalchbr.

Syn. : Euryporus Quél., Enchir., p. 163. 1886.

Characters : Pileus fibrillose to squamose, or even squarrose, the fibrils or scales not superimposed upon a viscid layer and therefore

even in wet weather except for *B. spectabilis* where the cuticle of the pileus becomes viscid starting from the margin and gelatinizing progressively towards the center; spores more or less elongate comparatively small to medium sized (up to 13.2 μ), pale melleous with occasional darker ones interspersed; cystidia voluminous and mostly covered by a resinous, colored incrustation; clamp connections potentially present in most species, i. e. at least some populations or carpophores of a species have at least some scattered clamps and in some species clamp-bearing specimens have not yet been found; hymenophore more (in the majority of the species) or less (especially in *B. amabilis, B. Benoisii*, and *B. pictus*) boletinoid, i. e. pores radiately arranged and radiately elongate, rather wide and compound, the radial walls of the tubes lamellae like, especially toward the stipe; hymenophore not lamellate at the very margin; stipe usually cylindric or subcylindric, more rarely fusoid or ventricosely swollen, etc., constantly without glandulae (some glandulae may however be seen on the pore edges if a lens is used); veil (Pl. XXV, 6 7) always present though not always persistent and not constantly forming an annulus, either simple or double and then the outer portion of the veil composed of a continuation of the covering of the pileus: mycelium connected with certain conifers (*Pinus, Larix, Picea, Pseudotsuga*) with which all species of *Boletinus* are associated, forming mycorrhiza. On the ground, more rarely on decayed wood, in woods and open places but then near coniferous trees or shrubs.

Development of the carpophores : Pseudoangiocarpous (*B. cavipes* according to Kühner, *B. spectabilis* and *B. pictus* according to Elrod & Snell; *B. decipiens*, gastroid forms (Pl. XXV, 5), are angiocarpous with, perhaps, a preceding gymnocarpous phase,

Area : Circumpolar, with the conifers in the conifer belt of the boreal and the temperate zone, only one species entering the subtropical zone with *Pinus*.

Limits : The limits separating *Boletinus* from *Suillus* have been frequently discussed by taxonomists, and various solutions have been proposed. The consent seems to be now that the presence or absence of clamp connections is not a generic character, yet if clamps are observed, the species is a *Boletinus*, if no clamps are observed, the species is either a *Boletinus* or a *Suillus*. It also appears that the configuration of the hymenophore is not of primary or decisive importance in the determination of the two genera. In fact, if a species has non boletinoid configuration, it is a *Suillus* (but three

species of *Boletinus* are intermediate), but if it has boletinoid configuration, it may be a *Boletinus*, or a *Suillus*. If a species has glandulae on the stipe, it is a *Suillus*. If it has no glandulae on the stipe it may be a *Boletinus*, but in may also be a *Suillus*. Species with entirely orange red to red or pink hymenophore are always *Suilli* (sect. *Piperati*), but the other colors do by no means prove the identity with *Boletinus*. A pileus, very glutinous in the center of young specimens will always indicate a *Suillus* but if the viscidity is weakly developed — as in some of the *Piperati* — this does not necessarily mean that the species belong in *Boletinus*. Only if a non-schematic approach is made, following the indications in the key, p. 648, a safe determination can be reached, and the resulting delimitation of *Boletinus* and *Suillus* is clear and natural. The hiatus between the two genera may not be very striking but it is not striking in any of the genera of the *Boletaceae*, yet it is present, as anyone who has enough experience with the groups involved, can corroborate. Even the beginner, if correctly instructed can easily seperate the two genera in the field which is often an indication of a « good » group, especially where the majority of the important characters are macroscopical.

State of knowledge : The genus has been studied monographically by Singer (*Revue de Mycologie* **3**, 1938, and *Farlowia* **2**, 1945) and most of the species are now completely known. The author admits twelve species as completely known, and three others as belonging in this genus but incompletely described.

Gastroid conditions of *Boletinus decipiens* (Berk.) Peck (Pl. XXV, 5), are of special interest for the systematist but, unfortunately, few collections have been made, and no living mycologist has collected fresh material of fertile gastroid carpophores. The dried material collected by R. Thaxter in Central Florida has been studied by the author. They are all smaller than the average size of *B. decipiens*. They do not open up in the way most *Agaricales* do, but remain closed and Gastromycete like all through their development which evidently is angiocarpous. Their shape is piriform; they have a columella (apex of the stipe) and labyrinthic loculi (hymenophore) confined to the lower side of the peridium (pileus) and producing spores which are of the same shape and the same size and color as those of the normal form of the *Boletinus*, viz. 7-9.5 × 3-3.8 μ, with the same thickness of the wall, and they originate on basidia which are in no way different from these of the pseudoangiocarpous form.

The spores are consequently heterotropic and axially asymmetric as all other spores of *Agaricales* are, and not as the majority of the spores of *Gastromycetes*. This is the main difference between this form and the genus *Truncocolumella* (*Dodgea*). The existence of gastroid forms in *Boletinus* is considered by C. Dodge, the author, and others as an additional evidence of the affinity of the boletes and the *Gastromycetes*, more precisely the group in which *Truncocolumella* belongs, i. e. the *Rhizopogonaceae*. As an intermediate form (half angiocarpous, as it seems) one would be inclined to cite *Gastroboletus* Lohwag. It would be very interesting to show experimentally or otherwise what precisely causes the aberrant carpophores to remain gastroid. This may throw some more light on the phylogenetic implications of this subject. Could it be that these carpophores were subjected to dry conditions while still in the primordial stage?

Practical importance: All species tested were found to be edible but they are moderately good food and not popular with the mushroom eaters.

In the author's opinion, both *Boletinus* and *Suillus* have a great potential importance in forestry. All species are mycorrhizal and to a greater or lesser degree specialized and selective as far as the mycorrhiza-host is concerned, never occurring without it. These fungi may become very important in reforestation projects.

SPECIES

Subgenus I. **Euboletinus** Sing. (1945). Hyphae constantly with numerous clamp connections; stipe sometimes hollow; mycorrhiza with *Larix*.

Type species: *B. cavipes* (Opat.) Kalchbr.

Sect. 1. CAVIPEDES Sing. (1938). Stipe hollow; pores truly boletinoid but not extremely wide as in *B. palustris*.

Type species: As in the subgenus.

B. cavipes (Opat.) Kalchbr.; *B. asiaticus* Sing.

Sect. 2. PALUSTRES Sing. (1938). Stipe solid; pores extremely wide.

Type species *B. paluster* (Peck) Peck.

B. paluster (Peck.) Peck.

Subgenus II. **Aporpiellus** Sing. (1945). Clamp connetions not present in all carpophores, and even if present, very scattered and

rare: stipe never hollow; mycorrhiza with larch or with other conifers.

Type species : *B. pictus* (Peck) Peck.

Sect. 3. **SPECTABILES** Sing. (1938). Veil duplex, the interior veil membranous and gelatinizing in the annulus and on the margin of the pileus (since the veil is of marginal origin), the exterior layer squamulose: hyphae of the epicutis of the pileus (outer layer of the veil) thin walled; mycorrhiza with *Larix*.

B. spectabilis Peck.

Sect. 4. **SOLIDIPEDES** Sing. (1938). Veil double or simple, never showing a gelatinization in any of its layers, the whole carpophore remaining dry, never viscid or scarcely so; pores as wide as in the *Cavipedes* or smaller (i. e. less distinctly boletinoid in some species); annulus frequently tending to become gray.

Type species : *B. pictus* (Peck) Peck.

B. pictus (Peck) Peck: *B. Benoisii* (Lebedeva ex) Sing.; *B. oxydabilis* Sing.; *B. grisellus* Peck; *B. ochraceoroseus* Snell; *B. amabilis* (Peck) Snell (and, if not indentical with the proceding species:) *B. Lakei* (Murr.) Sing. (Boletus, Murr.; Ixocomus, Sing. 1940); *B. decipiens* (Berk.) Peck; possibly also in this section: *B. appendiculatus* Peck, *B. solidipes* Peck, and *B. subgrisellus* Sing.

KEY TO THE SPECIES

A. Stipe hollow

B. Pileus carmine red. Altai to the Pacific Coast. *B. asiaticus*

B. Pileus not red. Circumpolar in the larch area. *B. cavipes*

A. Stipe not hollow, or eventually becoming slightly hollowed.

C. Small red species with enormously large pores; clamp connections constantly present. In bogs under larch in Eastern North America. *B. paluster*

C. Not combining these characters.

D. Pileus becoming at least partly viscid at maturity: large red species occurring under larch in bogs of Eastern North America. *B. spectabilis*

D. Pileus not or scarcely becoming viscid: pileus red or some other color; under larch or under other conifers.

E. Context distinctly and strongly (in young fresh specimens) changing color when bruised, annulus often gray or tending to become so; mycorrhiza with *Pinus*, or with *Larix sibirica* and *L. dahurica*; pileus « Vandyke red » to « Acajou red » (Ridgway), if growing with pine.

F. Mycorrhiza with *Pinus*. North America. *B. pictus*

F. Mycorrhiza with *Larix* in Asia.

G. Pileus deep [illegible] red to bright [illegible] red ; [illegible]

rhiza with *Larix dahurica* in Yakutia. *B. Benoisii*

G. Pileus merely with an occasional purplish brick shade; mycorrhiza with *Larix sibirica* in Oirotia. *B. oxydabilis*

E. Context slightly changing color over a limited area when bruised, or indistinctly and inconstantly discolored after rather long exposure to the air, or not changing at all; annulus not gray; pileus never entirely « Vandyke red » or « Acajou red »; fungi forming mycorrhiza with *Pinus*, *Larix* (but not *L. dahurica* or *L. sibirica*), *Pseudotsuga*, and *Picea*.

H. Mycorrhiza with *Larix occidentalis* and other species of *Larix*.

I. Spores around 4-5 µ broad; pileus never pinkish, North America. *B. grisellus*

I. Spores 3-3.5 µ broad; pileus inclined to be pinkish, Western North America. *B. ochraceoroseus*

H. Mycorrhiza with other conifers than *Larix*

J. Mycorrhiza with *Pseudotsuga* and *Picea*; species of Western North America.

K. Spores around 4.2 µ broad and (9.5) 11 (12.3) µ long. *B. amabilis*

K. Spores around 3.5 µ broad and (7) 8.5 (10.7) µ long. *B. Lakei*

J. Mycorrhiza with *Pinus*; species of the Eastern United States. *B. decipiens*

159. SUILLUS Micheli ex S. F. Gray

Nat. Arr. Brit. Pl. **1**: 646. 1821 em. Snell (1942).

Type species: *S. luteus* (L. ex Fr.) S. F. Gray.

Syn.: *Pinuzza* Micheli ex S. F. Gray, *Nat. Arr. Brit. Pl.* **1**: 646. 1821.
Rostkovites Karst., *Rev. Myc.* **3**: 16. 1881.
Cricunopus Karst., l. c.
Boletus Dill. ex Fr. sensu Karst., l. c., p. 17, non S. F. Gray (1821).
Viscipellis Quél., *Enchir.*, p. 155. 1886.
Versipellis Quél., l. c. p. 157, p. p.
Ixocomus Quél., *Fl. Mycol.*, p. 411. 1888.
Boletopsis Henn. in Engler & Prantl, *Nat. Pfl. fam.* **1** (1**): 194. 1898, non Fayod (1889).

Note: The type species and lectotypes accepted by the author see *Farlowia* **2**: 258-259. 1945. *Boletopsis* Henn. was not mentioned there; its lectotype should be *B. luteus* (L. ex Fr.) Henn.

Characters: Hyphae of the pellicle strongly gelatinized, and pileus in the center glutinous to subviscid from the beginning; spore print either between « ochraceous tawny » and « Isabella color », or rather

deep olivaceous; spores (Pl. XXV, 10), usually rather small but reaching about 14 µ in some species, rather pale colored, at least the majority; cystidia usually rather large and incrusted with resinous matter; tubes adnate to more rarely slightly depressed around the stipe, more often subdecurrent, rarely truly decurrent; pores very small to very wide and then usually boletinoid in arrangement, sometimes the pores as well as the interior of the tubes a rich orange red, or purplish red (rather dusky color) to pink; trama of the tube walls truly bilateral, of the *Boletus*-type, not of the *Phylloporus* type; stipe usually more or less cylindric, with or without glandulae (white, yellow, red, cinnamon, lilac, or black dots, consisting of fascicles of dermatocystidia, or of hyphae terminating in dermatocystidia of two types (Pl. XXV, 8 9), dermatopseudoparaphyses, and dermatobasidia); veil either present or absent, if present, consisting of gluten, or membranous and glutinous to viscid in wet weather; mycorrhiza with conifers exclusively except for one species with reddish pink hymenophore. Typically on the ground in woods and plantations.

Development of the carpophores: Pseudoangiocarpous (even in most evelate forms, e. gr. *S placidus, granulatus* ssp. *Snellii*, and *americanus* according to Elrod & Snell, but not in *S bovinus* according to Reijnders; the latter species is gymnocarpous).

Area: Temperate and boreal zone of the northern hemisphere and reaching the subtropical zone accompanying certain species of *Pinus*, also in some isolated alpine or montane regions of the tropics where *Pinus* occurs (Cuba, Java, etc.).

Limits: The *Suilli* differ from viscid species of *Pulveroboletus* either by the characters of the veil — which is bright yellow or orange and pulverulent in *Pulveroboletus* — or by forming mycorrhiza with conifers. Only one species may occur under frondose trees, and that one has reddish hymenophore, and all the other essential characters of the *Suilli* such as small, rather pale spores and large, incrusted cystidia; species with glandulae, or with boletinoid hymenophore are also never *Pulveroboleti* but always *Suilli*. Species with entirely red or pink hymenophore, and also such with viscid or glutinous veil do not refer to *Pulveroboletus* especially if the mycorrhiza is with conifers.

The only *Pulveroboletus* known to have a glutinous veil is *P. corrugatus*, a tropical species, not associated with conifers.

Similar characters, alternative characters, or combinations of characters separate *Suillus* from viscid species of other genera (*Xero-*

comus badius, and *X. brasiliensis*, *Boletus Frostii*, *Tylopilus plumbeo-violaceus*, *Leccinum rubropunctum*, etc.) of the *Boletaceae* and *Boletellus* of the *Strobilomycetaceae*. But the difficulty in practice is not so great here as it is in separating *Pulveroboletus* from *Suillus*, since all the other genera, in addition to the data given above, also differ in habit or anatomically.

State of knowledge : This genus is probably not yet completely known since there are pine populations with a flora of ectotrophic mycorrhiza in certain parts of the world where the *Suillus* symbionts have never been studied taxonomically, and in many cases the latter have not even been collected. Nevertheless, the genus appears to be comparatively well known since all the European and most of the American species have been studied very thoroughly with enough emphasis on previously neglected characters such as the dermatocystidia of the stipe, the exact color of the spore print, and the chemical color reactions. In addition, the American flora lends itself well to ecological studies, and field observations on the degree of selectiveness of each species in nature are very interesting. Outside Europe and North America, the flora of the Altai Mts. in Central Asia is one of the regions whose *Suillus* flora is nearly completely known; for a while it seemed to be known better than the *Suillus*-flora of the Alps, and it is perhaps still better known than the *Suillus* flora of the Rocky Mountain region.

The author recognizes 28 species.

Practical importance : This genus is perhaps the most interesting one in regard of mycorrhiza investigations. It will undoubtedly play a major role in future developments of forestry, i. e. as soon as the schools of forestry begin to give more attention to this vital factor, especially in forest pathology and reforestation projects. *Suillus* seems to be particulary important for pine and larch. Besides, the genus *Suillus* contains several very valuable edible mushrooms, some of them widely used in Europe and Asia, also sold in the markets, and pickled by various companies for domestic and foreign consumption.

SPECIES

Sect. 1. LARIGNI Sing. (1938). Annulus usually well developed; stipe without glandular dots; hymenophore yellow, grayish white, orange rusty red, etc. Symbiosis with *Larix*.

Type species : S. Grevillei (Klotzsch) Sing.

Subsect. **Megaporini** Sing. (1938). Pores wide, often boletinoid, larger than 1 mm in diameter when fully mature

Type species : S. aeruginascens (Secr.) Snell.

S. aeruginascens (Secr.) Snell (Boletus, Secr.; Boletus viscidus L (?) ex Fr.; Ixocomus, Quél.; Boletus laricinus Berk.; Boletus larignus Britz.; Boletus elbensis Peck); *S. flavus* (With. ex Fr. sensu Bres., Nüesch) Sing. (Boletus, Fr.; Ixocomus, Sing. 1938); *S. tridentinus* (Bres. Sing. (Boletus, Bres.; Ixocomus, Sing. 1938).

Subsect. **Microporini** Sing. (1938). Pores small (diameter less than 1 mm).

Type species : As in section 1.

S. Grevillei (Klotzsch) Sing. [Boletus, Klotzsch; Boletus flavus var. elegans (Schum. ex) Fr.; Ixocomus flavus var. elegans Quel.; Ixocomus elegans Sing.] with var. *Clintonianus* (Peck) Sing. (Boletus Clintonianus Peck); also *S. jacuticus* (Sing.) Sing. (Ixocomus, Sing.) unless it belongs in subsection *Macroporini*.

Sect. 2. **GRANULATI** Sing. (1938). Stipe with glandular dots, rarely with indistinct and scattered minute glandulae (and macroscopically appearing devoid of glandulae) and then stipe initially pure white, or pores with conspicuous glandulae; hymenophore not reddish or pink; symbiosis with *Pinus*, rarely with *Tsuga, Abies*, perhaps also *Pseudotsuga* and *Picea*, never with *Larix*.

Type species : S. luteus (L. ex Fr.) S. F. Gray.

Subsect. **Latiporini** Sing. (1938). Spore print cinnamon; pores wide, often boletinoid, larger than 1 mm in tangential diameter when fully mature.

Type species : S. flavidus (Fr.) Sing.

S. flavidus (Fr.) Sing. (Boletus, Fr.); *S. sibiricus* (Sing.) Sing. (Ixocomus, Sing), with ssp. *helveticus* Sing. (Ixocomus sibiricus sensu Favre non Sing.); *S. glandulosus* (Peck) Sing. (Boletinus, Peck); *S. americanus* (Peck) Snell (Boletus, Peck); *S. subaureus* (Peck) Snell (Boletus, Peck); probably also *S. flavoluteus* (Snell) Sing. (Boletinus, Snell) if distinct from *S. americanus*.

Subsect. **Angustiporini** Sing. (1938). Spore print cinnamon; pores usually smaller than 1 mm in diameter, rarely reaching 1 mm in fully mature specimens.

Type species : S. granulatus (L. ex Fr.) O. Kuntze.

S. subluteus (Peck) Snell apud Slipp & Snell (Boletus, Peck,; *S. cothurnatus* Sing. with two seasonally dimorphous subspecies, ssp.

aestivalis Sing., and ssp. *hiemalis* Sing., *S. luteus* (L. ex Fr.) S. F. Gray (Boletus, L. ex Fr.; Ixocomus, Quel.); *S. placidus* (Bon.) Sing. (Boletus, Bon.; Ixocomus, Sing.; Boletus albus Peck); *S. granulatus* (L. ex Fr.) O. Kuntze, with ssp. *typicus* and ssp. *leptopus* (Pers.) Sing. and ssp. *Snellii* Sing. (the latter identical with most American material of « *Boletus granulatus* », the former a Mediterranean race, described and collected as *Boletus* and *Ixocomus Bellinii*, *Boletus* and *Ixocomus Boudieri* [1], and *Ixocomus leptopus* by the different authors); *S. albidipes* (Peck) Sing. (Boletus, Peck); *S. brevipes* (Peck) O. Kuntze (with several varieties); perhaps also *S. acidus* (Peck) Sing. (Boletus, Peck).

Subsect. Hirtellini Sing. (1945). Spore print brown with a later vanishing olivaceous tinge; pileus fibrillosely rough to squamulose (innately so, not from the superficial veil); pores small to medium wide (i. e. their diameter smaller than 1 mm. or around 1 mm.).

Type species : S. hirtellus (Peck) O. Kuntze.

S. punctipes (Peck) Sing. (Boletus, Peck); *S. plorans* (Rolland) Sing. (Boletus, Rolland; Ixocomus, Favre; Boletus Cembrae Studer); *S. tomentosus* (Kauffm.) Sing. (Boletus, Kauffm.; S. hirtellus var. mutans (Peck ex) Snell apud Slipp & Snell); *S. Cembrae* (Sing.) Sing. (Ixocomus, Sing.); *S. hirtellus* (Peck) O. Kuntze (Boletus Peck); *S. ruber* Sing. & Sipe apud Sing.

Sect. 3. BOVINI Sing. (1938). Stipe without glandular dots; colored from the beginning; veil none; pores not pink and not red, also not orange rusty, but often becoming pinkish on drying; mycorrhiza with *Pinus*, more rarely with other conifers.

Type species : S. bovinus (L. ex Fr.) O. Kuntze.

Subsect. Euryporini Sing. (1938). Pores wide (more than 1 mm. in diameter); pileus not squamulose; context with ammonia becoming dark rose, then red, and eventually brownish vinaceous.

S. bovinus (L. ex Fr.) O. Kuntze.

Subsect. Stenosporini Sing. (1938). Pores small to medium sized (diameter 1 mm. or slightly less); pileus squamulose as in the *Granulati* subsection *Hirtellini*; context reacting more indistinctly (reddish-lilac) with ammonia.

[1] One cannot help but suspect that the two species which Reichert (*Stud. Mushr. Palestine* I, in *Pal. Journ. Bot.* 3 (1-2): 209-224. 1940) attempts to keep apart under the names *Rostkovites Boudieri* (Quél.) Reichert and *R. Bellinii* (Inz.) Reichert, are merely different stages, the latter representing a younger, or perhaps retarded condition of the carpophore, but both specifically identical

S. variegatus (Sw. ex Fr.) O. Kuntze.

Sect. 4. **PIPERATI** Sing. (1938). Stipe without glandular dots, colored from the beginning; veil none; surface of the pileus moderately viscid to almost dry, glabrous or squamulose-flocculose; hymenophore dull purplish red or dull red inside, and outside, or pink throughout, or sometimes partly red or pink but the red or pink color never localized at the pores only, eventually often disappearing in very old specimens; mycelium at the base of the stipe tending to be yellow, forming mycorrhiza with various trees, mostly conifers (*Picea*, *Abies*, more rarely *Tsuga*, *Pseudotsuga*, or *Pinus*), but occasionally also with frondose trees [114].

Type species : S. piperatus (Bull. ex Fr.) O. Kuntze.

S. rubinus (W. G. Smith) Sing. (Boletus, W. G. Smith); *S. piperatus* (Bull. ex Fr.) O. Kuntze, with var. *amarellus* (Quél.) Sing. (Boletus Pierrhuguesii Boud.); *S. rubinellus* (Peck) Sing. (Boletus, Peck).

KEY TO THE SPECIES

A. Stipe with a veil and without glandular dots; mycorrhiza with larch

B. Pileus raspberry red. Northeast Asia. *S. paluticus*

B. Pileus some other color.

C. Pores wide, yellow when young and not injured, Alps, Altai, possibly England (where it might have been introduced with seedlings) *S. flavus*

C. Pores either not yellow, or not wide.

D. Pores yellow, small (less than 1 mm. in diameter). *S. Grevillei*

D. Pores not yellow.

E. Pores orange russet Alps and most of Europe, Altai and most of Siberia. *S tridentinus*

E Pores whitish then grayish. Circumpolar. *S aeruginascens*

A. Stipe with or without veil; if a veil is present, the stipe is beset with glandular dots; mycorrhiza not with *Larix*.

F. Stipe with glandular dots.

[114] There can be no doubt but that *Boletus rubinus* as described by the British mycologists, especially Pearson who has studied this species more carefully than his predecessors, is a species of this section of *Suillus*, yet, the habitat as indicated in the literature is not with conifers which is a very unusual case in this whole subfamily Mr. A. A Pearson, Hindhead, Surrey, England, was kind enough to write me about the habitat of this fungus: « In one case there are no coniferous trees in the neighborhood; in the other, there was a recent plantation of firs but on the other side of a brook and ravine that intervened Both were under oaks and that is the habitat mentioned by Rea. »

G. Spore print cinnamon without the slightest olivaceous tinge even when quite fresh; pileus smooth and glabrous except for occasional superficial floccons or patches from the veil; reaction with ammonia always distinct.

H. Many pores more than 1 mm. in diameter, often boletinoid; veil present but often fugacious.

I. Pileus bright golden yellow. North America, mostly with *Pinus strobus*. *S. americanus*

I. Pileus dull yellow, olivaceous-alutaceous, etc.

J. Annulus hyaline at first and completely glutinous-slimy. In moist woods and swamps in Europe under *Pinus silvestris*. *S. flavidus*

J. Annulus not so and not occurring under *Pinus silvestris*.

K. With *Pinus* ssp.

L. Pileus umbonate; annulus usually present. Occurring with various pines from the American Pacific Coast region east to the Lake Athabasca region in Canada, and also in the Altai and in the Alps (here a subspecies *helveticus*). *S. sibiricus*

L. Pileus obtuse, or exceptionally umbonate; annulus absent. North America. *S. subaureus*

K. With other conifers. Northeastern North America. *S. glandulosus*

H. Pores all less than 1 mm in diameter.

M. Glandulae manifest.

N. Veil present.

O. Stipe about 6 times longer than thick, or more; annulus not broadly sheathing; mycorrhiza with *Pinus*, sect. *Cembrae* in North America. *S. sublutens*

O. Stipe shorter, or annulus broadly sheathing; mycorrhiza usually with pines of other sections than *Cembrae* (2-3 needle-pines).

P. Context a warm orange yellow; annulus very strikingly broadly sheathing the stipe; mycorrhiza with *Pinus taeda*, *P. palustris*, and *P. australis* in southeastern North America. *S. cothurnatus*

P. Context white to partially lemon yellow; annulus somewhat sheathing in its lower portion, distant above when normally developed; mycorrhiza in nature with *P. pinea*, *P. silvestris*, *P. nigra*, *P. mugho*, *P. resinosa*. Circumpolar. *S. luteus*

N. Veil present and then never forming an annulus, or else absent, more frequently absent.

Q. Pileus white or at least partly white for a long

period, stipe elongate and usually much longer than the diameter of the pileus; NH_4OH reaction red in mature specimens; mycorrhiza with *Pinus*, sect. *Cembrae*. Eastern North America and Europe. *S. placidus*

Q. Pileus differently colored, or stipe shorter and not occurring under pines of the section *Cembrae*.

R. Spores larger than 8.2 μ (at least a majority of spores in a print reaching higher figures). European, Asiatic and African races of *S. granulatus*.

S. Stipe elongate; pileus yellow to yellowish brown; mycorrhiza with *Pinus silvestris* and *P. mugho*. Europe, Western Siberia, etc. *S. granulatus* ssp. *typicus*

S. Stipe short; pileus often whitish or light fuscous. mycorrhiza with Mediterranean pines. Mediterranean region from Spain to Palestine. *S. granulatus* ssp. *leptopus*

R. Spores all shorter than 8.2 μ, or just reaching 8.2 μ.

T. Glandulae conspicuous, not limited to the apex of the stipe in fresh mature material; tubes adnate; veil rarely present; stipe without reddish colors inside under normal weather conditions; mycorrhiza with *Pinus strobus* in North America *S. granulatus* ssp. *Snellii*

T. Glandulae confined to the apex of the stipe, minute; tubes decurrent in most specimens when mature; veil marginal, usually rather distinct; mycorrhiza with *Pinus strobus* and *P. monticola*, sometimes also in nearby stands of other pines, or other conifers. North America *S. albidipes*

M. Glandulae very indistinct or practically absent; stipe initially white, usually short; mycorrhiza usually with « two-needle pines » in North America (if stipe long, cf. *S. albidipes*). *S. brevipes*

G. Spore print with an olivaceous tinge.

U. Context unchanging, or at least not becoming blue on exposure; stipe very slightly and gradually tapering toward the apex, or almost perfectly equal.

V. Basal mycelium pink; pores brownish or rather deep ocher-brown. European species under *Pinus cembra*.

W. Stipe strongly thickened toward the base; pores brownish to brownish olive, never yellow; glandulae crowded, often running into each other and making the stipe sticky; numerous non incrusted fusoid cystidia present on the pores; spores (7.8) 8.8-11.5 x 3-3.7 µ; color of the pileus often around « Mars yellow »; mycelium white; NH_4OH and NH_3 on the surface of the pileus definitely negative. With pines, mostly *P. strobus*, in North America. *S. punctipes*

W. Stipe slightly, if at all, thickened toward the base; pores of immature and mature carpophores yellow, or pinkish ocher (in youth), or yellowish olive (in age); glandulae distinct and numerous but not forming sticky patches; non incrusted cystidia infrequent on the pores; fusoid cystidia exceptional, or none; spores (6.8) 7.5-10.2 × 3-3.5 µ; color of the pileus never «Mars yellow»; mycelium not always white; NH_3 on disc of pileus « Persian lilac », on margin « Acajou red » (Ridgway) after very long exposure; NH_4OH lilac, then purplish carmine, then amethyst around an eventually cinnamon spot. With pines in North America. *S. hirtellus*

U. Context bluing; stipe more or less thickened toward the base, sometimes rather abruptly thickened.

X. Pileus red. Oregon. *S. ruber*

X. Pileus not red.

Y. Pileus and stipe golden yellow, then sulphur yellow to sordid yellowish cream, rather dull colored in herbarium material; mycelium white; « in several associations of the *Thuja-Tsuga* zone » (Slipp & Snell). North America, Rocky Mts., and west to the Pacific Coast. *S. tomentosus*

Y. Pileus ocher-brownish to orange brownish with darker squamules; mycelium pink; in *Larix-Pinus-Picea* stands of the north-exposed slopes of the Central Alps. *S. cembrae*

F. Stipe without glandulae.

Z. Stipe at first pure white. (see *S. brevipes*)

Z. Stipe colored from the beginning.

AA. Pores and tubes reddish (dull purplish red, dull red, pink, etc.) when quite fresh (even partly so, but not merely the pores discolorous).

BB. Spores ellipsoid, short; reported under oaks in England. *S. rubinus*

BB. Spores more elongate, always under conifers.

CC. Pileus warty floccose; taste mild. Eastern North America. *S. rubinellus*

CC. Pileus glabrous; taste mild or peppery. Circumpolar. *S. piperatus*

151. PHYLLOPORUS Quél.

Flore Mycol., p. 409. 1888.

Type species : *P. Pelletieri* (Lév. apud Crouan) Quél. [= *P. rhodoxanthus* (Schw.) Bres. ssp. *europaeus* Sing.].

Characters : All characters as in the subfamily but the hymenophore lamellate (with anastomoses in most cases) ; the cuticle of the pileus when young and fresh always turning vivid blue with ammoniacal vapors ; hymenophoral trama always with a lateral stratum consisting of hyphae touching each other (not very loosely arranged) and moderately strongly divergent, not or not much paler colored than the mediostratum, i. e. constantly of the *Phylloporus*-type, and never even intermediate between the *Phylloporus* type and the *Boletus* type. On the ground, rarely on very decayed wood, under trees.

Development of the carpophores : Unknown.

Area : Almost cosmopolitan, but rarer in Northern Asia and some other regions than in Southeastern Asia, North America and parts of Europe.

Limits : This genus differs from other agarics by the bright blue reaction caused by ammonia on the surface of the pileus ; only a few species of *Xerocomus* have the same reaction. The genus *Xerocomus* is distinguished by tubulose hymenophore.

The author found it most practical to follow the example of Quélet himself who is the original author of both genera, *Phylloporus* and *Xerocomus*, and consequently, all tubulose species are taken to *Xerocomus*. On the other hand, one might prefer to combine the section *Pseudophyllopori* of *Xerocomus* with the genus *Phylloporus*, thus basing the delimitation primarily on the chemical characters. This would not materially improve the delimitation as compared with that proposed by Quélet and the author, and therefore was rejected in view of the readiness by which the configuration of the hymenophore can be ascertained as compared with the observation of a chemical color reaction which is often obscured by age, and absent in dried material.

State of knowledge : There is only one species which is completely known. But this species has been split into a « circle of races », representing a sum of subspecies. These geographic races were all characterized and some of them described by the author (*Farlowia* **2** : 280-284. 1945). Another, Indian, species is known to the author from dried material.

Practical importance : Unknown.

SPECIES AND SUBSPECIES

P. rhodoxanthus (Schw.) Bres. (Gomphidius, Sacc.; Flammula, Lloyd; Paxillus, Ricken) consisting of ssp. *americanus* Sing. (the type subspecies, also Paxillus flavidus Berk.; perhaps Paxillus sulcatus Pat.), ssp. *bogoriensis* (Hoehnel) Sing (P. bogoriensis Hoehnel); ssp. *europaeus* Sing. [P. Pelletieri (Lév. apud Crouan) Quel.; Clitocybe, Gillet; Paxillus, Vel.; Paxillus paradoxus (Kalchbr). Cooke]; ssp. *foliiporus* (Murr.) Sing. (Gomphidius foliiporus Murr.): *P. sulphureus* (Berk.) Sing. (Paxillus, Berk.). Perhaps also *P. infundibuliformis* (Cleland) Sing. (Paxillus, Cleland).

152. XEROCOMUS Quél.

Flore Mycol., p. 417, 1888.

Type species : *X. subtomentosus* (L. ex Fr.) Quél.

Syn. : *Xerocomopsis* Reichert, *Palest. Journ. Bot. Reh. Ser.*, 3 : 229 1940

Characters : Pileus more or less tomentose or subtomentose, frequently with at least fragmentary trichodermium palisade; hymenophore not lamellate, occasionally subboletinoid but never truly boletinoid, most frequently with rather wide and angular pores, adnate, often with a decurrent tooth, or arcuate-decurrent, more rarely becoming depressed around the stipe and then usually the radial walls of the tubes forming a sublamellate ring around the apex of the stipe, not free, but sometimes separating in age; spores variable in size, subcylindric to subfusoid, or ellipsoid-oblong to ellipsoid-subclavate, sometimes almost ellipsoid-ovoid and rather short; always olivaceous brown in print; hymenophoral trama of the *Phylloporus* type (*Phylloporus*-subtype of the bilateral type), i. e. lateral stratum consisting of moderately diverging and not very loosely arranged hyphae, not much or not at all paler than the mediostratum, in section *Pseudoboleti* the structure of the trama intermediate between the *Phylloporus*-subtype and the *Boletus*-subtype (hyphae of the lateral stratum distinctly divergent, looser than in the mediostratum but still mostly touching each other, hyphae of the mediostratum slightly subparallel-sub-interwoven and slightly colored, deeper than the practically hyaline lateral stratum); cystidia medium-sized to rather large, not strikingly

none; stipe usually cylindric, or subequal and comparatively rather thin, more rarely assuming some other shape, and very rarely ventricose-bulbous as in *Boletus*, sometimes with an ocher-brown to chestnut colored coarse network at the apex of the stipe, never finely reticulated as in *Boletus*; veil none; yellow pulverulence none; glutinous covering of stipe or pileus absent; context unchanging or changing color, often bluing in certain portions; all hyphae without clamp connections. On soil, humus, very decayed wood, anthills, and carpophores of *Scleroderma*, in the woods, and in gardens near trees.

Development of the carpophores: Gymnocarpous in *X. Zelleri* (Zeller 1914); slightly hemiangiocarpous in *X. parasiticus* (Reijnders 1933; cf. Singer 1945).

Area: Almost cosmopolitan.

Limits: Some species of the section *Pseudophyllopori* are so similar to *Phylloporus* that it is difficult to tell them apart without knowing the configuration of the hymenophore. The blue ammonia reaction is also the same in those two groups. On the other hand, the section *Pseudoboleti* is so close to *Boletus*, it is sometimes difficult to tell the difference without a very careful analysis of the structure of the hymenophoral trama and a comparison of the average habit and the chemical characters of the species concerned. It is conceivable that some mycologists would prefer to combine *Xerocomus* and *Boletus*, but then, there would be no way of avoiding the disappearance of *Phylloporus*, and as a result, we would find *Phylloporus* — a genus considered as belonging to *Paxillus* by most of the authors of the Friesian era — and *Boletus edulis, B. appendiculatus*, etc. side by side in the same genus. We have here a case parallel and comparable taxonomically with that of the Mycenas and that of the Clitocybes, the former as well as the latter either covering their own subtribes and becoming monster genera in size and divergence of the extremes unless they are divided in smaller natural units. In the case of the *Phylloporus Xerocomus Boletus*-complex, the author believes that these three genera are natural elements, and should be preserved in the sense applied to them in the present work. This still leaves the door open for minor corrections if such should later appear to be necessary, e. gr. the transfer of the *Pseudophyllopori* to *Phylloporus*, or the *Pseudoboleti* to *Boletus*, etc. No such transfers are warranted at the present time, nor are they likely to become necessary in the future unless new data and facts turn up that are not foreseeable now.

State of knowledge : Since the sections of the genus are based on chemical and anatomical characters, it is to be expected that many species must still be considered as incompletely known, i. e. one or two characters are missing which would provide the data required for an insertion in the scheme of sections proposed by the author. Consequently, the number of species admitted here is no indication of the actual number of species which is probably much higher than the total of 14 inserted in the classification plus the 4 species admitted as being species of *Xerocomus.* Even so, the position of some species in their respective sections is rather a temporary one since the chemical reactions are unknown in some of the species admitted. In section 1, the author (1945) arbitrarily introduced a sectional diagnosis containing as the main characterization a chemical reaction but with an alternative microscopical feature, the shape of the spores. This made it possible to insert several species into the system of classification adopted by the author such as would otherwise have remained on the list of doubtful species. But this whole arrangement did not necessarily provide the permanent definition of the section *Pseudophyllopori*, but merely a temporary one. At least some of the short spored species had to be removed from this section when the ammonia reaction of fresh material became known.

Practical importance : It is not known wheter all species of *Xerocomus* are mycorrhizal fungi, and the practical importance they might have if they were mycorrhizal, is only potential at the time being. Besides, most species seem to be selective as to the mycorrhiza host but to a certain degree, much less so than the species of *Suillus* and *Boletinus.* All species tested have proved to be edible, especially *X. subtomentosus* and *X. chrysenteron* which are frequently used for food and even sold in the markets of Europe.

SPECIES

Sect. 1. **PSEUDOPHYLLOPORI** Sing. (1945). Ammonia reaction bright and rich blue on the young, fresh pilei (« porcelain blue» or « dusky green blue » of Ridgway).

Type species : X. illudens (Peck) Sing.

X. hypoxanthus Sing.; *X. pseudoboletinus* (Murr.) Sing. (Ceriomyces, Murr.); *X. hemixanthus* Sing.; *X. illudens* (Peck) Sing. (Boletus, Peck) with var. *xanthomycelinus* Sing.; probably also the following:

X. lanatus (Rostk.) Sing. (Boletus, Rostk.) and *X. coniferarum* Sing. [Boletus ferrugineus Bres. non Frost; X. spadiceus (Fr. sensu Quélet) Quél.; possibly *X. Linderi* Sing. (reactions unknown)].

Sect. 2. **PSEUDOGYRODONTES** Sing. Ammonia reaction not as indicated above; spores always short (twice as long as broad or shorter): pores and tubes not yellow, more or less arcuate decurrent.

Type species: X. squarrosoides (Snell & Dick) Sing.

X. squarrosoides (Snell & Dick) Sing. (Boletus, Snell & Dick; Phylloporus, Sing. 1938); most probably also *X. Housei* (Murr.) (Ceriomyces, Murr.).

Sect. 3. **SUBTOMENTOSI** (Fr.) Sing. (1942). Spores elongate, i. e. more than twice as long as broad; reaction with ammonia on the surface of the pileus never as indicated in section 1, but either negative, or indistinctly livid, violet, blackish blue, chestnut color, these colors (except the latter) often not persistent but disappearing within a second; mycelium never parasitic on the carpophores of gastromycetes (*Scleroderma*); trama truly characteristic of the *Phylloporus* subtype of bilaterality; pileus not tomentose and viscid at the same time, in fact rarely viscid in the species known.

Type species: X. subtomentosus (L. ex Fr.) Quél.

X. subtomentosus (L. ex Fr.) Quel. (Boletus, L. ex Fr.); *X. chrysenteron* (Bull. ex Fr.) Quel. (Boletus, Bull. ex Fr.); *X. Zelleri* (Murr.) Snell apud Slipp & Snell (Ceriomyces, Murr.) (if not conspecific with the preceding species); probably also *X. Junghuhnii* (Hoehnel) Sing. (Boletus, Hoehnel).

Sect. 4. **PARASITICI** Sing. (1942). As in the preceding section but growing parasitically on the carpophores of *Scleroderma* (perhaps occasionally also on other fungi); context not or scarcely bluing; trama of the *Phylloporus* subtype.

X. parasiticus (Bull. ex Fr.) Quel. (Boletus, Bull. ex. Fr.).

Sect. 5. **BRASILIENSES** Sing. (1945). Pileus tomentose and viscid at the same time; pores initially rather small, then becoming large or, comparatively, gigantic; spores small (6-9.3 × 2.8-4.2 µ); otherwise as in the *Subtomentosi*.

Type species: X. brasiliensis (Rick) Sing.

X. brasiliensis (Rick) Sing. (Boletus, Rick); obviously also *X. indicus* Sing.

Sect. 6 **PSEUDOBOLETI** Sing. (1945). Pileus somewhat viscid or dry and tomentose, depending on the amount of humidity absorbed, or granulose-floccose; tramal structure intermediate between

the *Phylloporus* subtype and the *Boletus*-subtype ; ammonia provoking a blackish blue reaction on fresh and young specimens (surface of the pileus), but this reaction disappears very rapidly, exactly as the same reaction in section 3 ; spores rather large (11.5-18.5 (24) × 4-5.7 μ ; pores medium wide, rather pale colored with a greenish tinge or pale yellowish. On the ground in woods (coniferous or frondose).

Type species : *X. badius* (Fr.) Kühner ex Gilbert.

X. badius (Fr.) Kühner ex Gilbert (Boletus, Fr.) ; *X. Roxanae* (Frost) Sing. (Boletus, Frost) ; obviously also *X. Boudieri* Sing. (Boletus leoninus Boudier non Krombh.).

KEY TO THE SPECIES

See Singer, *Farlowia* **2** : 287-288. 1945.

Subfamily **Boletoideae** Sing.

Am. Midl. Natur. **37** : 1. 1947

Type genus : Boletus Dill. ex Fr. em. Sing. (1947).

Characters : Pileus viscid or dry ; stipe equal or ventricose-bulbous, viscid or dry ; veil present or absent ; if present, either pulverulent and yellow or orange-latericious or green, or else entirely glutinous ; clamp connections always constantly and completely absent ; glandulae none ; hymenophoral trama always of the *Boletus* subtype of the bilateral type, i. e. the lateral stratum consisting of loosely arranged, strongly divergent hyphae which are much paler (mostly hyaline) than the mediostratum ; hymenophore never red or pink both inside and outside. Mycorrhiza not exclusively with conifers, but some species or subspecies forming mycorrhiza with conifers.

Note : The *Boletoideae* represent a very natural group of genera wich are all closely related to each other. Their most remarkable links with other groups can be found in *Pulveroboletus* which, perhaps, approaches *Suillus*, and *Boletus*, section *Subpruinosi* Fr. which seems to be close to *Xerocomus*, sect. *Pseudoboleti*. While *Phlebopus* may be considered as the most primitive group of the series, *Leccinum* is probably the most highly developed genus.

KEY TO THE GENERA

A. Stipe not scabrous, i. e. not beset with darker or concolorous (and then yellow) squamules or furfuraceous particles, or else, i. e. if the stipe is somewhat furfuraceous, the pores are reddish, or the cuticle is neiter a cutis nor an epithelium; the surface of the stipe is also often smooth, pubescent, finely reticulate to coarsely reticulate or somewhat longitudinally fibrillose, or pulverulent; pores small or wide, red or concolorous, free or adnate to somewhat decurrent; mycorrhiza with frondose trees or with coniferous trees, in some cases the formation of mycorrhiza not certain.

B. Spore print consistently brownish with an olivaceous tinge, or olive colored.

C. Pileus covered with a yellow pulverulence or viscid (and then the cuticle not made up of an epithelium or trichodermium), veil often present, or stipe viscid, in very old and dried material, the hymenophore often assuming a very deep golden yellow or golden olive, or reddish orange color due to an easily dissolved (NH_4OH) pigment which is bright yellow under the microscope and similar to that of the *Gymnopils* (*Cortinariaceae*).

D. Hymenophore a thin to medium thick layer of decurrent tubes, arcuate at least when young; stipe frequently swollen-ventricose and sometimes forrowed at the base which often arises from a pseudosclerotium, context frequently turning blue on exposure; veil none; size of the carpophores often remarkable.

153. *Phlebopus*

D. Hymenophore consisting of rather long tubes, not decurrent but either adnate or depressed around the stipe, either applanate or convex beneath; stipe usually not swollen-ventricose but in most species and specimens either subequal or attenuate toward the apex or toward the base; pseudosclerotium none; context rarely turning blue, and if it does, there is a yellow pulverulence present (from the veil); carpophores small to large.

154. *Pulveroboletus*

C. Pileus not covered with yellow pulverulence and not viscid unless the cuticle is made up by a trichodermium; veil never present; stipe always dry; yellow pigment often present but usually not as abundant and deep colored as in *Gymnopilus*. 155. *Boletus*

B. Spore print not showing any trace of olive even if quite fresh.

E. Spore print rusty yellow; spores bright golden under the microscope, long-cylindric, almost rod shaped and narrow in the type; stipe smooth and glabrous; context white, unchanging, mild

156. *Xanthoconium*

E. Spore print deeper ferruginous brown, or wood brown, fawn color, pinkish vinaceous, etc., spores not golden under the microscope, not (or exceptionally) rod shaped; stipe rarely smooth and glabrous as well; context rarely white and unchanging and mild at the same time. 157. *Tylopilus*

A. Stipe scabrous with darker squamules or furfuraceous particles, the squamules

somewhat squarrulose, making the surface appear rough, and consisting of fascicles of parallel hyphae which end up in a fragmentary stipe hymenium, consisting of dermatobasidia, dermato pseudoparaphyses, and dermatocystidia; if the surface of the stipe is merely forfuraceous, the cuticle consists partly of an epithelium or a cutis (cinnamon colored horizontal hyphae imbedded in a gelatinous mass); stipe often rather fibrous hard and often attenuate from the basal thickening to the apex, more rarely cylindric or ventricose; pores of the hymenophore very small, their walls thin, therefore also the hymenophoral trama a very thin layer, the pores never red, the tubes free or very strongly depressed around the apex of the stipe, very long in most species in the middle between the apex of the stipe and the margin; mycorrhiza almost constantly with trees of the orders *Salicales* or *Fagales* (only in *Leccinum aurantiacum* occasionally with 2-needle pines, but much more frequently with *Populus*). 158. *Leccinum*

153. PHLEBOPUS (Heim) Sing.

Ann. Mycol. 34 : 326. 1936.

Type species : *P. colossus* (Heim) Sing.

Syn. : *Boletus* subgenus *Phlebopus* Heim, *Rev. Mycol.* 1 : 6. 1936.

Characters : Hymenophore arcuate, tubes decurrent in young carpophores and remaining so for a considerable period, rather short; stipe frequently swollen ventricose and sometimes furrowed at the base which often arises from a pseudosclerotium; context frequently turning blue on exposure; veil none; size of the carpophores often remarkable; otherwise much like *Pulveroboletus*. On the ground in woods, on various débris, on stumps and trunks, on sawdust, etc.

Development of the carpophores : Unknown.

Area : African and Asiatic tropics, only one species in Europe and North America.

Limits : In habit, this genus is close to *Gyrodon* but lacking the clamp connections. In the other characters it is close to *Pulveroboletus* but differs in habit.

State of knowledge : The most essential characters are known in three species.

Practical importance : The tropical species are suspected to be poisonous.

SPECIES

Sect. 1. COLOSSI Sing. (1947). Stipe furrowed near the base.

P. colossus (Heim) Sing.

Sect. 2. **SULPHUREI** Sing. (1947). Stipe scarcely furrowed or quite smooth.

Type species: *P. sulphureus* (Fr.) Sing.

P. sulphureus (Fr.) Sing. (Boletus, Fr., Boletus hemichrysus Berk. & Curt.); *P. viperinus* Sing.

KEY TO THE SPECIES

This genus is still small, and a key is not urgently needed; however, if a key is wanted, it can be consulted in Singer, *Am. Midl. Natur.* **37**: 23. 1947.

154. PULVEROBOLETUS Murr.

Mycologia **1**: 9. 1909, em. Sing. (1947).

Type species: *P. Ravenelii* (Berk. & Curt.) Murr.

Characters: Pileus viscid when wet, dry when observed in dry weather; cuticle most frequently consisting of a cutis, more rarely of a trichodermium, often covered with the slender appressed hyphae of the superficial yellow pulverulence (veil), this pulverulence or veil sometimes more green or reddish than yellow but never whitish or gray, brown, etc.; veil, if present, having a pulverulent arachnoid consistency, not viscid, or, in one species completely glutinous and hyaline; if there is no veil, there are nevertheless traces or rudiments of a veil in form of a glutinous or pulverulent sheathing of the stipe, rarely veil not apparent at all; stipe either entirely smooth, or sometimes reticulate, usually subcylindric or somewhat thickened at the base but not typically bulbous-ventricose or swollen-ventricose; tubes not or scarcely arcuate when the carpophores are very young, later applanate or convex beneath, usually more or less depressed around the stipe, usually comparatively long (one fifteenth of the diameter of the pileus in large specimens, or longer), the longest tubes situated in the middle between the margin and the stipe, often very bright golden yellow, or reddish orange, or golden olive, colors never observed in *Boletus*, and persisting after drying, or even appearing on drying: they are due to a very soluble (NH_4OH) pigment which is yellow and rapidly permeates the whole preparation but disappears after a few minutes when agitated; pores small to large; hymenophoral trama truly bilateral divergent of the *Boletus*-subtype but the difference between lateral stratum and mediostratum not always very strongly expressed in preparations made in NH_4OH

medium because of the solubility of the pigment; clamp connections none; spores typically elongate and either fusoid or ellipsoid fusoid to subcylindric, more rarely short cylindric or short ellipsoid; cystidia usually rather large with the upper portion broadly inflated, or else rather thin and ampullaceous; spore print olivaceous brown (« Isabella color », « olive citrine », « medal bronze », etc. Ridway, or plate 16, 12 C, Maerz & Paul); context bluing only if a yellow pulverulent veil is present. On the soil in woods, and near trees, with coniferous as well as with frondose trees.

Development of the carpophores: Unknown

Area: Most abundatly occurring in North America and in south eastern Asia, but also in Africa, Europe, and perhaps almost cosmopolitan.

Limits: The limits against *Xerocomus* are determined by the structure of the trama. The species with intermediate tramal structure (sect. *Pseudoboleti* of *Xerocomus*) are not similar to *Pulveroboletus*, and their chemical reactions separate them, especially the ammonia reaction which is generally much stronger in the *Xerocomi* than in the *Pulveroboleti*. The *Xerocomi* never have any viscidity or any pulverulent veil on the stipe. In the section *Pseudoboleti*, there is never any reticulation on the middle portion of the stipe whereas *P. retipes* has a very strong reticulation.

The *Pulveroboleti* differ from *Suillus* in often having viscid but evelate stipe, a combination not known in *Suillus*, also, in having the characteristic bright and rich yellow pigment in the hymenophore (but not in all species), in forming mycorrhiza with frondose trees (as well as with conifers). Dusky red to pink color of the hymenophore occurs only in *Suillus*; golden yellow, orange-scarlet, or olive golden hymenophore, especially if well preserved in dried specimens indicates *Pulveroboletus*. *Pulveroboletus* has no glandulae, and no viscid veil (except in *P. corrugatus*).

The *Boleti* in the narrowest sense differ from *Pulveroboletus* in the characters indicated in the key, but in certain cases, one may have difficulties in the determination. This concerns species without veil and viscosity and with reticulated stipe in *Pulveroboletus*, and species with smooth stipe in *Boletus*. Consequently, one would consider *Pulveroboletus retipes* as close to *Boletus*, and *Boletus Atkinsonianus* as close to *Pulveroboletus*. The former reminds one of *Boletus auripes* in *Boletus*, and the latter reminds one of *Pulveroboletus Curtisii* in *Pulveroboletus*. A similar pair is *Boletus subsolitarius* and *Pulveroboletus*

caespitosus. The distribution of these species between *Pulveroboletus* and *Boletus* may appear somewhat arbitrary, but it is based on the main affinities of a given species and the sum of its characters rather than on the weight of a single character, *Pulveroboletus retipes* was put in *Pulveroboletus* because of the pulverulent margin often observed in this species, and also because of its cuticular structure. *P. Curtisii* is certainly a *Pulveroboletus* because of its general appearance, viscid stipe, etc. and the viscid to glutinose stipe of *P. caespitosus* and its affinity with *P. auriporus* show clearly enough that this species belongs in *Pulveroboletus*, not in *Boletus*. The genus *Pulveroboletus*, in the emended limits is undoubtedly a very natural genus, as anyone will appreciate who assembles a good field and laboratory knowledge of this interesting group. Minor questions as to where exactly the natural hiatus between this genus and *Boletus* must be sought, will be decided after some more monographic studies have made this possible. It is possible that *Pulveroboletus retipes* will eventually be reunited with *Boletus*.

State of knowledge : The species belonging here are well known, at least those occurring in North America, and those Asiatic species whose type specimens could be studied. There is only one species in Europe. The author admits 12 species.

Practical importance : Some species are edible but most are of mediocre quality. Very little is known about their mycorrhizal relationships, but it may be assumed that they have some potential value in forestry just as *Xerocomus* and *Boletus*.

SPECIES

Sect. 1. **FLAVOVELATI** Sing. (1947). Veil pulverulent arachnoid, sulphureous, or greenish, not viscid, distinct.

Type species : *P. Ravenelii* (Berk. & Curt.) Murr.

P. Ravenelii (Berk. & Curt.) Murr. (Boletus, B. & C.; Boletopsis ictcrinus Pat. & Baker), and perhaps *Boletus subglobosus* Cleland & Cheer.

Sect. 2. **RETICULATI** Sing. (1947). Pileus and stipe often yellow or orange pulverulent but pulverulence inconstant and not forming a veil; stipe not viscid, strongly reticulate.

Type species : *P. auriflammeus* (Berk. & Curt.) Sing.

P. auriflammeus (Berk. & Curt.) Sing. (Boletus, B. & C. ; *P. retipes*

(Berk. & Curt.) Sing. (Boletus, B. & C.; Boletus ornatipes Peck).

Sect. 3. **AURIPORI** (Sing.) Sing. (1947) (*Xerocomus* sect. *Auripori* Sing. 1942). Pores golden yellow or brightly olive gold even in dried condition; veil either not abundant, or absent, yellow-pulverulent if present; either pileus or stipe or both viscid; elements of the trama often filled with deep lemon yellow soluble (NH_4OH) pigment.

Type species: *P. auriporus* (Peck) Sing.

P. subacidus (Murr. ex) Sing. (Ceriomyces, Murr., nom. nud.); *P. auriporus* (Peck) Sing. (Boletus, Peck); *P. caespitosus* (Peck) Sing. (Boletus, Peck); *P. gentilis* (Quél.) Sing. (Boletus sanguineus var. gentilis Quél.); *P. flaviporus* (Earle) Sing. (Boletus, Earle).

Sect. 4. **CARTILAGINEI** Sing. (1947). Veil none; hymenophore not persistently golden yellow nor orange nor golden olive; stipe not or scarcely reticulate, rarely subreticulate in part, more or less fleshy cartilaginous, rather frequently hollow; context mostly or always unchanging. Tropical species, or temperate southern species.

Type species: *P. Curtisii* (Berk.) Sing.

P. Curtisii (Berk.) Sing. (Boletus, Berk.); *P. rufobadius* (Bres.) Sing. (Boletus, Bres.); *P. viscidulus* (Pat. & Baker) Sing. (Boletus, Pat. & Baker); *P. phaeocephalus* (Pat. & Baker) Sing. (Boletus, Pat. & Baker).

KEY TO THE SPECIES

A key taking into consideration all the species indicated above has been published by Singer, *Am. Midl. Natur.* **37**: 7-12. 1947. Nothing can be added to this key at present.

135. **BOLETUS** Dill. ex Fr.

Syst. Mycol. **1**: 385. 1821, sensu str. Gilbert (1931) non al.

Type species: ***B. edulis*** **Bull. ex Fr.**

Syn.: *Tubiporus* Paulet ex Karst., *Rev. Mycol.* **3**: 16. 1881.
Dictyopus Quél., *Enchir.* p. 159. 1886.
Oedipus Bat., *Bolets*, p. 13. 1908.
Suillellus Murr., *Mycologia* **1**: 16. 1909.
Ceriomyces Batt. ex Murr., *Mycologia* **1**: 144. 1909.

Characters: Cuticle (Pl. XXVI, 1-5) of the pileus rarely (in small tropical species) an epithelium; hymenophore consisting of small or large pores continuing into long tubes, depressed to almost free around the stipe in most specimens; hymenophoral trama truly

bilateral-divergent of the *Boletus* subtype; spore print olive or at least brown with an olive hue when quite fresh («olive brown», «dark olive buff», «brownish olive», between «citrine drab» and «deep olive»); spores usually elongate (with variable shape), but in some (especially tropical) species short; stipe usually thick and fleshy and solid, reticulate or finely flocculose-squamulose subfurfuraceous, rarely smooth and glabrous, neither scabrous not glandulose, evelate, without a distinct pseudosclerotium; context white or yellow, sometimes partly red, on injury often bluing, rarely reddening, mild or bitter; all hyphae without clamp connections. On the ground in woods and near trees.

Development of the carpophores: Probably gymnocarpous but not known in detail from recent investigations.

Area: Cosmopolitan, but most strongly represented in the warmer parts of the temperate zones, especially in America and perhaps in Asia.

Limits: As for the separation of *Boletus* from the preceding genera, see there. *Boletus* is well separated from *Tylopilus* in spite of what some European authors say about it. They know only one single species of *Tylopilus* and are not in a position to judge on the hiatus between the two groups. Aside from the color of the spore print which is sharply different in the two genera, there is also a difference in the darkening of the context in those species that are subject to autoxidation. This autoxidation provokes bluing in *Boletus*, and a variety of discolorations (reddish gray, vinaceous, lilac, etc.) but no bluing in *Tylopilus*. *Boletus* is also well separated from *Xanthoconium* by the color and shape of the spores. In *Leccinum*, most of the species have the spore color of *Boletus* (or somewhat less olive). They are separated from *Boletus* by the roughness of their stipe. In some species with yellow pigment (sect. *Luteoscabra* of *Leccinum*) the scabrosities of *Leccinum* may be rather similar to the surface ornamentation of some *Boletus*-stipes. In this particular case, the author has taken to *Leccinum* the species with a definite cutis and viscid pileus as well as the species with an epithelium, while the species with trichodermium (Pl. XXVI, 1-4) and dry pileus remain in *Boletus*. Naturally, in some species of *Boletus*, the trichodermium forms a palisade (Pl. XXVI, 2 4) and the single members of the chains may become very short, and on the other hand in some specimens of *Leccinum rugosiceps*, the spherocysts of the epithelium may be somewhat elongated. In spite of such minor variations, the sepa-

ration on this basis is rather sharp, and it leaves only a small number of species with epithelium in *Boletus*, and these are minute (Pl. XXVI, 9), tropical, and not at all related to *Leccinum*. All species that may possibly be construed as intermediate between *Leccinum* and *Boletus*, are thus taken care of.

State of knowledge : Some interesting details are still missing in the descriptions of certain species, especially in the difficult *Edules*-group, and also in the *Calopedes* and in the *Luridi*. However, the general knowledge on the genus is now rather satisfactory in America, and nearly as good in Europe. More data are needed on Asiatic, Australian, and African representatives of the genus. Forty eight species have been admitted.

Practical importance : Concerning their mycorrhizal properties, the *Boleti* have the same chances as the neighboring genera to become interesting in forestry. At present, the main practical importance of the species of *Boletus* is their edibility. *B. edulis*, and *B. aereus* belong to the most widely used and traded wild mushrooms in the world, at least as far as the temperate zones are concerned. They are exported from Eastern Europe to various parts of the world, in dried as well as in pickled form. Fresh « cèpes », « hriby », and « Herrenpilze » are found in all European markets at the proper season but all efforts to grow them commercially have failed. Other species of this genus — as far as they have mild taste — are also highly estimated by mycophagists, but some species of the section *Calopodes* can spoil a whole meal by their bitterness. They should be carefully avoided. There have been controversies about the poisonous properties of *B. luridus*, *B. satanas*, and *B. miniatoolivaceus* (the three most poisonous species), and the response of various persons to the action of the poison as well as the violence of the poison itself varies a great deal. Even the three species named above are at times harmless. But if eaten by certain persons at certain localities in a certain quantity, even a small one, and especially if not cooked thoroughly, they may cause very serious poisonings. Phoebus published one case with *B. satanas*, where he himself had tested the species, and the symptoms are much the same as those experienced by the author when he had eaten *Boletus luridus :* Rapid action of the poison, excessive vomiting, psychological symptoms (depression), fast recovery.

Two species have thus far been proved to have antibacterial properties : *B. radicans* and *B. satanas*.

SPECIES

Sect. 1. **EDULES** Fr. (1938). Context white and unchanging (or at least not bluing except in very rare cases in which a slight bluing is observed near the tubes), mild; stipe quite smooth to distinctly reticulate; spores elongate; epicutis (Pl. XXVI, 1 2) not an epithelium, tubes white, later yellowish, then greenish in some species, or pores occasionally slightly brownish; cystidia not strongly colored.

Type species: B. edulis Bull. ex Fr.

B. Atkinsonianus (Murr.) Sacc. & Trotter; *B. olivaceobrunneus* Zeller; *B. edulis* Bull. ex Fr. with several subspecies (geographic races and myco-ecologic adaptations of a permanent, hereditary type); *B. separans* Peck; *B. aereus* Bull. ex Fr.

Sect. 2. **GRISEI** (Sing. 1947) (*Xerocomus*, sect. *Grisei* Sing. 1942). Tubes white, layer, greyish; cystidia strongly colored (melleous or fuscous or brown), otherwise much like the preceding section.

Type species: B. griseus Frost apud Peck.

B. griseus (Frost apud Peck), ssp. *typicus* and ssp. *Pini caribaeae* Sing.; *B. fumosiceps* (Murr.) Sing.

Sect. 3. **CALOPODES** Fr. (1938), sensu str. Sing. (*Pachypodes* Konr. & Maubl. 1924-37). Context white to yellowish, bitter; tube wall bluing when fresh.

Type species: B. calopus Fr.

B. frustosus Snell. & Dick; *B. radicans* Pers. ex Fr. sensu Kallenbach (B. albidus Rocqu.); *B. inedulis* (Murr.) Murr.; *B. calopus* Fr.; *B. Peckii* Frost apud Peck; *B. pallidus* Frost.

Sect. 4. **APPENDICULATI** Konr. & Maubl. (1924-37). Context more or less yellow, bluing or unchanging, mild, not bitter; stipe distinctly but finely reticulate; pores not or scarcely discolorous, never red; context not containing poisonous substances; pileus never viscid.

Type species: B. appendiculatus Schaeff. ex Fr.

B. auripes Peck; *B. appendiculatus* Schaeff. ex Fr.; *B. pallescens* (Konrad) Sing. (Boletus appendiculatus ssp. pallescens Konrad); *B. speciosus* Frost; *B. regius* Krombh.

Sect. 5. **SUBPRUINOSI** Fr. (1874) em. Sing. (1947). Network on the stipe none or consisting of a narrow reticulate zone of decurrent pores immediately under the hymenophore, usually finely flocculose to furfuraceous, or fibrillose; context mild, changing or unchanging,

more often bluing then not changing, never becoming pinkish gray or vinaceous, not containing poisonous substances in any known species; carpophores small (Pl. XXVI, 9) to medium sized, rarely large and with the habit of a *Xerocomus* rather than a *Boletus* (stipe not very thick and not ventricose or not much so); hymenophore adnate or slightly depressed around the stipe, more rarely deeply depressed, the pores medium sized (1 mm) to large in age, either distinctly open or daedaleoid meandering and folded when young; surface of the pileus usually tomentose, or pruinose, or subtomentose, or velutinous, or granular.

Type species : B. Barlae Fr. (= *B. rubellus* Krombh.).

B. peruanus Pat. & Baker (this and perhaps the following species belong in a well defined group, perhaps a new section, characterized by the presence of an epithelium on the pileus); *B. Patouillardii* Sing.; *B. nanus* Masee; *B. aureomycelinus* Pat. & Baker; *B. Weberi* Sing. (this species and perhaps *B. parvus* Peck, belong in a well defined group, perhaps a separate section, characterized by red pores); *B. pulverulentus* Opat. (B. mutabilis Morgan); *B. granulosiceps* Sing.; *B. subsolitarius* Sing.; *B. rubellus* Krombh. (B. versicolor Rostk. non S. F. Gray; B. sanguineus With. non L. ex Lév. in Paulet, non Secr.; B. rubripruinosus Barla; B. bicolor Peck; B. Barlae Fr.; B. rubeus Frost; B. fraternus Peck; Xerocomus pruinatus Quél.) with several subspecies (geographic races and mycoecotypes).

Sect. 6. LURIDI Fr. (1838). Differs from the preceding section in smaller pores and generally more typical *Boletus*-habit in contrast to the *Xerocomus* habit of most of the species of sect. *Subpruinosi*; pores more often discolorous; surface of the stipe as in the preceding section but in some species finely to very strongly reticulate; pileus with a covering as indicated in the preceding section, or viscid; context often containing poisonous matter.

Type species : B. luridus Schaeff. ex Fr.

B. impolitus Fr.; *B. rubricitrinus* (Murr.) Murr.; *B. luridellus* (Murr.) Murr. (Ceriomyces subsensibilis Murr.); *B. oliveisporus* (Murr.) Murr.; *B. flavissimus* (Murr.) Murr.; *B. miniatoolivaceus* Frost with var. *subluridus* (Murr.) Sing. (Suillellus subluridus Murr.); *B. junquilleus* (Quél.) Boudier; *B. Queletii* Schulzer; *B. Dupainii* Boudier; *B. austrinus* Sing.; *B. tomentipes* Earle; *B. hypocarycinus* Sing.; *B. subvelutipes* Peck; *B. vermiculosus* Peck; *B. erythropus* (Fr. ex Fr.) Pers.; *B. Morrisii* Peck; *B. Eastwoodiae* (Murr.) Sacc.

& Trotter; *B. rhodoxanthus* (Krombh.) Kallenbach; *B. satanas* Lenz; *B. luridus* Schaeff. ex Fr.; *B. Frostii* Russel with ssp. *floridanus* Sing.; probably also *B. dichrous* Ellis, *B. Sullivantii* Berk. & Curt. apud Mont., *B. magnisporus* Frost. and *B. firmus* Frost.

KEY TO THE SPECIES

Keys to the various sections of *Boletus* applicable to European and Eastern North American, especially Floridian species but also to all other species sufficiently well known at present can be found in Singer, *Am. Midl. Natur.* **37**: 21-60. 1947.

156. XANTHOCONIUM Sing.

Mycologia **36**: 361. 1944.

Type species: *X. stramineum* (Murr.) Sing.

Characters: Pileus not scrobiculate; hymenophore consisting of medium long, white to yellow tubes with small pores, the latter concolorus, plainly adnate or adnexed, or more frequently depressed around the apex of the stipe; spores in print «antique brown», «raw sienna», or «Sudan brown» to «Argus brown» (Ridgway), or «Antique bronze», «burnished gold», «chipmonk» (Maerz & Paul), often more yellowish in thin layer, and more dull fuscous where they were in contact with the carpophore, bright golden under the microscope, cylindric to rod shaped (Pl. XXVI, 8), or fusoid cylindric and always rather narrow, smooth, with thin walls; cystidia present in the tubes and on the pores; hymenophoral trama truly bilateral-divergent of the *Boletus* subtype; stipe equal or ventricose, rather thick, glabrous or subglabrous, completely smooth, solid; context white, unchanging, mild. On the ground in woods but not specific for coniferous or frondose trees, and found to be associated with either of these.

Development of the carpophores: Unknown.

Area: Temperate and subtropical North America.

Limits: Clearly separable from *Boletus* and *Tylopilus*. The color of the spores and the white, mild, unchanging context correlated with non scrobiculate pileus separate it from *Tylopilus*. The color (in print and under the microscope) of the spores separate it from *Boletus*; the shape of the spores may also serve as an auxiliary character. The yellow spored species of the *Gyrodontoideae* differ in having clamp connections, much shorter and less rusty colored spores which are not golden under the microscope.

State of knowledge : Two species are known.

Practical importance. Both species are edible. They may have some potential importance in forestry since they are mycorrhizal, as far as field observations can indicate.

SPECIES

X. stramineum (Murr.) Sing. (Gyroporus, Murr.); *X. affine* (Peck) Sing. (Boletus, Peck).

157. TYLOPILUS Karst.

Rev. Mycol. **3** : 16. 1881.

Type species. *T. felleus* (Bull. ex Fr.) Karst.

Syn. : *Rhodoporus* (Quél.) Bat. *Bolets*, p. 11. 1908
Leucogyroporus Snell, *Mycologia* **34** : 408. 1942
? *Rhodoboletes* G. Beck, *Zeitschr. Pilzk.* **2** : 146. 1923

Characters : Pileus subglabrous to tomentose, sometimes scrobiculate, dry or viscid, cuticle of diverse structures, even sometimes cellular; hymenophore light colored or pallid at least when young, usually depressed around the stipe, at least at maturity; pores small, not discolorous at the pore mouths except by autoxidation when injured: spore print ranging from a sordid pinkish flesh color to dull flesh ocher, wood brown, deep ferruginous brown, etc. (« Light russet vinaceous », « russet vinaceous », « Rood's brown », « fawn color », « army brown », between « wood brown » and « fawn color », « pinkish cinnamon » with a shade of « fawn color », « vinaceous fawn », « cream buff », « Isabella color » or « chamois » without an olive shade, « amber brown », etc. All these colors are indicated in Ridgway terms), often becoming paler after prolonged preservation in the herbarium, pale melleous to melleous-subhyaline, or brownish-pallid to stramineous under the microscope, variable in shape, smooth, thin walled; cystidia usually well developed, sometimes strongly contrasting with the hyaline basidia; hymenophoral trama truly bilateral divergent of the *Boletus* subtype; stipe either naked or covered with a palisade of hairs or dermatocystidia, often with a hymenium in the reticulate portions which are rather extensive in some species; veil none; context whitish, never yellow, unchanging, or changing when exposed to the oxygen of the air but never bluing,

mild to the taste, or bitter, but mild and unchanging only in one species (*T. conicus* — with scrobiculate pileus). On the ground in woods, probably always forming mycorrhiza with forest trees but rarely selective in regard to the mycorrhiza partner. Spores and or trama sometimes slightly amyloid.

Development of the carpophores : Unknown.

Area : Probably almost cosmopolitan; occurs even through the whole of Siberia (where most species of *Boletus* are absent because of the scarcity of broad leaved trees).

Limits : The differentiation of this genus is complete. Though *Boletus*, *Xanthoconium*, and *Leccinum* are closely related, they are easily separable, and the hiatus dividing these genera from each other is satisfactory.

Leccinum, sect. *Roseoscabra* has a similar spore print, and may be considered as the only link between *Leccinum* and *Tylopilus*. It differs from all species of *Tylopilus* in having the typical scabrous stipe of the *Leccina*.

Some authors have confused this genus with *Porphyrellus*. The difference between the two genera will be pointed out in the latter genus, p. 693.

State of knowledge All species occurring in Europe (only one) and North America are well known to the taxonomists (see Singer, *Am. Midl. Natur.* 37: 89-110. 1947). Some species from southeastern Asia are also known as far as their most essential features are concerned. The same is true for Africa. The number of species admitted is 15.

Practical importance : Some species are edible, others are non-edible and often spoil a mushroom meal because of their bitter taste. They may become interesting for the forester since they are probably all mycorrhizal fungi.

SPECIES

Sect. 1. **FELLEI** Sing. (1947). Context unchanging, more or less bitter to almost mild, not staining yellow with KOH; pileus not scrobiculate, spore print pinkish (e. gr. « French beige », « rose beige », Maerz & Paul).

Type species : *T. felleus* (Bull. ex Fr.) Karst.

T. Rhoadsiae (Murr.) Murr.; *T. minor* Sing.; *T. felleus* (Bull. ex Fr.) Karst.; *T. plumbeoviolaceus* (Snell) Snell.

Sect. 2. SCROBICULATI Sing (1947). Pileus scrobiculate; context mild, white, unchanging but staining yellowish with KOH; stipe white, smooth.

T. conicus (Rav. apud. Berk. & Curt.) Beardslee (Boletus, Rav apud B. & C.).

Sect. 3. OXYDABILES Sing. (1947). Pileus not scrobiculate; context turning violet or reddish or gray when bruised, strongly reacting with KOH, bitter or mild.

Type species: T. tabacinus (Peck) Sing.

T. Balloui (Peck) Sing. (Boletus, Peck); *T. veluticeps* (Pat. & Baker) Sing. (Boletus, Pat. & Baker); *T. cellulosus* Sing; *T. nigricans* (Pat. & Baker) Sing. (Boletus, Pat. & Baker); *T. alboater* (Schw.) Murr. (Boletus, Schw.; Porphyrellus, Gilbert; Boletus nigrellus Peck; Porphyrellus, Gilbert); *T. eximius* (Peck) Sing. (Boletus, Peck); *T. ferrugineus* (Frost) Sing. (Boletus, Frost); *T. tabacinus* (Peck) Sing. (Boletus, Peck) with several varieties; *T. peralbidus* (Snell & Beardslee) Murr. (Boletus, Snell & Beardslee) with var. *rhodoconius* Sing.; *T. appalachiensis* Sing. (Tylopilus felleus var. minor Coker & Beers nom. subnud.); perhaps also *Ceriomyces alachuanus* Murr., *Boletus modestus* Peck, and *Tylopilus javanicus* Henn.

KEY TO THE SPECIES

See Singer in *Am. Midl. Natur.* **37**: 90 and 97. 1947.

158. LECCINUM S. F. Gray

Nat. Arr. Brit. Pl. **1**: 646. 1821, em. Snell (1942)

Type species: L. aurantiacum (Bull. ex) S. F. Gray.

Syn.: *Krombholzia* Karst. *Rev. Mycol.* **3**: 17. 1881 non Rupr. ex Galeotti (1844) nec *Krombholzia* Benth. (1881)
Trachypus Bat., *Boleti* p. 12. 1908 non Reinw. & Hornsch. (1826)
Krombholziella R. Maire, *Publ. Inst. Bot. Barcelona* **3** (4): 41. 1935

Characters: Pileus with a cuticle consisting of an epithelium (Pl. XXVI, 7) or with only a few spherocysts, or with some chains of broad and short hyphae mixed in along with filamentous hyphae of a trichodermium, or the cuticle made up by a cutis consisting of filamentous horizontally arranged hyphae at least in the upper stratum, viscid or dry, glabrous, granulose, or tomentose, often rimose or rimulose areolate, the margin often sterile and membranous,

projecting as a continuation of the cuticle and the marginal trama (and sometimes misinterpreted as an appendiculate veil); hymenophore yellow or yellowish, or whitish to sordid, convex beneath, the tubes very long in comparison with the diameter of the context and the radius of the pileus, but drastically shortened around the stipe and almost free, or free when adult, pores very fine to small (less than 1 mm in diameter) and the walls between the tubes also very thin (consequently also the trama a very thin layer); pores never discolorous but sometimes stained because of discoloration from autoxidation after injury; hymenophoral trama truly bilateral divergent of the *Boletus* subtype; spore print olivaceous umber to umber, « olive brown » (Ridgway) to « Clove » (Maerz & Paul) or (in one section) sordid vinaceous wood brown (« burnt almond » to « Tuscan » Maerz & Paul); spores under the microscope always fusoid cylindric or fusoid ellipsoid, strongly elongated and rather large in most species (often reaching more than 20 µ in several species); cystidia fusoid ventricose, very frequently with an ampullaceous apex, hyaline, small to medium sized; stipe usually rather thin and fragile at the very apex, gradually becoming thicker toward the base, often fibrous hard at the base, scabrous from darker squarrose squamules or from strongly projecting furfuraceous ornamentations, the scabrosities sometimes connected by a very fine network, consisting of dermatobasidia, dermatopseudoparaphyses, and dermatocystidia which terminate fasciculately a bunch of parallel hyaline hyphae, without glandulae, never sticky, viscid, or glutinous, but consistently dry, evelate, without pseudosclerotium; mycelium directly connected with mycorrhiza of *Salicales* and *Fagales*, rarely (in a minority of cases in *L. aurantiacum* in North America) with *Pinus rigida*, etc.; context yellow or white, changing or unchanging, often blue in the base of the stipe, otherwise not blue or bluing except in one rare variety of *L. subglabripes*; all hyphae without clamp connections. On the ground in woods and near trees (*Salix*, *Populus*, *Betula*, *Carpinus*, *Fagus*, *Quercus*, etc.).

Development of the carpophore : Not studied in detail by any recent author.

Area : From the arctic regions to the subtropics in the northern hemisphere, absent in the tropics except for the higher mountain ranges (e. gr. Guatemala); most species and individuals in Eastern North America.

Limits : See under *Boletus* and *Tylopilus*.

State of knowledge: The genus *Leccinum* is comparatively well known, including the chemical reactions. More data are needed on a few species, e. gr. *L. nigrescens*, *L. corsicus* and *L. oxydabilis* where the delimitation of the species and the geographic distribution are still imperfectly known. Other problems left to be solved in *Leccinum* are rather of intraspecific nature such as the study of the forms and races of *L. aurantiacum* and *L. scabrum*. A further elucidation of this problem may lead to an explanation of the strange ecologic behavior, in certain regions, of *L. aurantiacum* or what must be identified as such according to our present knowledge.

The author admits 12 species.

Practical importance: The genus *Leccinum* is very important as an article of export from Eastern Europe, especially from the U. S. S. R. The species are widely used in local markets, and also by amateurs, for use in fresh condition as well as dried or salted, or pickled for use later in the winter. This applies for Eastern Europe as well as for other regions of Europe and for Northern Asia.

The *Leccina* may also become important for forestry since all of them are very specialized mycorrhizal fungi.

SPECIES

Sect. 1. LUTEOSCABRA Sing. (1947). Hymenophore and usually also stipe and at least a part of the context yellow or yellowish; spore print « olive brown » (Ridgway) or some similar color with a distinct olive tinge.

Type species: *L. nigrescens* (Richon & Roze) Sing.

L. subglabripes (Peck) Sing. (Boletus, Peck); *L. rugosiceps* (Peck) Sing. (Boletus, Peck); *L. nigrescens* (Richon & Roze) Sing. (Boletus, Richon & Roze; Boletus tesselatus Gillet non Rostkov.; Boletus luteoporus Bouchinot apud Barbier; Krombholzia, Sing.; Phylloporus platensis Speg.); *L. rubropunctum* (Peck) Sing. (Boletus, Peck); probably also *Boletus corsicus* Rolland (Boletus sardous Belli & Sacc.; Boletus tlemcenensis R. Maire).

Sect. 2. VERSIPELLES (Fr. 1838, em. Konr. & Maubl. 1924 37) Sing. (1947). Hymenophore not yellow; stipe yellow at the base in certain specimens but not otherwise; context yellow at the base in many specimens but not otherwise; spore print olive umber brown to umber e. gr. « Clove » (Maerz & Paul).

Type species: Boletus versipellis Fr. (which is probably for the most part *L. aurantiacum*, and possibly partly *L. testaceoscabrum*).

L. albellum (Peck) Sing. (Boletus, Peck); *L. duriusculum* (Schulzer apud Fr.) Sing. sensu Sing. [1] [Boletus, Schulzer apud Fr. ex diagn.; Gyroporus griseus Quél. ex diagn.; Boletus pseudoscaber Kallenbach non Secr.; Boletus nigrescens Huber non Richon & Roze; Boletus Carpini (R. Schultz) Pearson]; *L. oxydabile* Sing. Sing. (Krombholzia, Sing.); *L. chalybaeum* Sing.; *L. aurantiacum* (Bull. ex) S. F. Gray (Boletus, Bull. ex Pers.; Boletus versipellis Fr. max. e parte; Leccinum, Snell apud Slipp & Snell; Boletus rufus Schaeff. ex aut. nonn. p. p.); *L. testaceoscabrum* (Secr.) Sing. (Boletus testaceus scaber Secr.; Boletus rufescens scaber Secr.; Boletus rufescens «Secr.», Konrad; Krombholzia rufescens Sing. 1938); *L. scabrum* (Bull. ex Fr.) S. F. Gray (Boletus scaber Bull. ex Fr.; Krombholzia, Karst.; Ceriomyces viscidus Murr.) with several forms and subspecies, especially ssp. *rotundifoliae* (Sing.) Sing. and ssp. *niveum* (Fr.) Sing. [Boletus scaber ssp. niveus (Fr.) Konrad].

Sect. 3. **ROSEOSCABRA** Sing. (1947). Differs from the preceding section in even deeper (chrome) yellow base and, mainly, in the color of the spore print which lacks the olivaceous or umber hue, and is more like what is called «pink» in *Tylopilus*, i. e. «burnt almond» or «Tuscan tan» of Maerz & Paul.

L. chromapes (Frost) Sing. (Boletus, Frost).

KEY TO THE SPECIES

A key to the perfectly known species of this genus has been published by Singer in *Am. Midl. Natur.* **37**: 111, 112, 118-119, 1947.

GENERA INCERTAE SEDIS

Boletochaete Sing., *Mycologia* **36**: 358. 1944. «Genus of the *Boletaceae*; spores under the microscope brownish hyaline or melleous-brownish, smooth, fusoid-ellipsoid or ovoid-ellipsoid; basidia not voluminous; cystidia numerous; hymenial setae numerous; hymenophoral trama subregular (not distinctly bilateral) in adult specimens; hyphae without clamp connections; hymenophore tubulose, adnexed; stipe cylindric to ventricose.» Singer. The type species is

[1] The type of *B. duriusculus* does not exist in Budapest.

Boletus spinifer Pat. & Baker. The type of this species has short spores. A species with elongate spores is *Boletochaete brunneosetosa* Sing. and another one is the *Xerocomus* sp. mentioned by Heim, *Bol. Soc. Brot.* 13: 53. 1938.

The genus is very distinctive, and can easily be recognized in dried material. The setuloid cystidia (or « setae ») are always colored not by an incrustation as cystidia are likely to be, but by a membrana-pigment, and their walls are thick. Since no young specimens were available which would have shown the structure of the trama, the genus could not be inserted in the classification as outlined above. It may be expected that the hymenophoral trama is of the *Boletus*-subtype.

Ixechinus Heim, *Rev. Myc.* 4: 20. 1939. « Gymnocarpous (?) species, small to medium sized, entirely gelatinous by humidity; pileus continuous with the stipe, with entire margin and glabrous vestiment: stipe central, slender ... more or less striate ribbed, not reticulate, solid; hymenophore naked, depressed distant from the stipe, formed by ... very long, fleshy-elastic, entirely free from each other ... tubes, which are individually separable from the context of the pileus; pores always open, small, rounded, light colored; context ... not bluing ...; spores amygdaliform elongate or narrowly cylindric, smooth, pale citrinous ochraceous; ... cystidia fusoid attenuate, thin-walled. On the soil, forming mycorrhiza. Madagascar. » Heim [14].

Two closely allied species are known as belonging here, *I. majus* and *I. minus* Heim. The hymenophoral trama of these species is shown by Heim to be bilateral but it may represent a third subtype of bilaterality among the boletes which may be called « *Ixechinus*-subtype » characterized by still more gelatinized lateral trama than that of the *Boletus* subtype. Figure 2 in Heim's paper shows no clamp connections, but this is not conclusive since it is not definitely stated in the text. The exact color of the spore print and the chemical reactions are also unknown, or at least unpublished. This is certainly an interesting genus provided that the separation of the tubes occurs regularly in nature. Its final place in the classification of the *Boletaceae* is difficult to indicate at present. A special tribus, *Ixechineae* Heim, has been proposed by Heim.

Fistulinella Henn., *Engler's Bot. Jahrb.* 30: 43. 1901. « Pileus fleshy.

[14] This diagnosis has been slightly shortened, and some terms have been adapted to the terminology applied in this book.

stipitate, margin velate membranous; hymenium porous; tubes cylindric, almost free from each other and separated ». The type species is *F. Staudtii* Henn. from tropical West Africa. Heim compares this genus with his own *Ixechinus,* and concludes that the two genera are different. However, Henning'species is so poorly described, and has never been restudied, that a final judgment is almost impossible. If the type should have been lost, this genus will probably be considered as a nomen dubium. Otherwise a comparison of the types of *F. Staudtii* and *Ixechinus minus* and *I. majus* would be very interesting.

Gastroboletus Lohwag, *Beih. Bot. Centralbl.* **42** (2): 273. 1926. « Small, reminiscent of a Gastromycete in its habit; pileate and stipitate; pileus as in *Secotium*: stipe little shorter and with the base of the pileus partly connected, hymenophore tubulose. » Lohwag. This is based on one species, *G. Boedijnii* Lohwag which in spite of its unique half angiocarpous character, is in need of a more thorough examination. It would be interesting to know the structure of the hymenophoral trama, the hyphae (whether there are clamp connections present), the color of the spore print, the character of the cystidia (if there are any), and many other things neglected in the diagnosis. It may well be that *Gastroboletus* is close to the gastromycetous genus *Truncocolumella.* It has been collected only in northwestern Yunnan, China.

STROBILOMYCETACEAE Gilbert

Boletes, p. 83, 105. 1931 (ut *Strobilomyceteae*); Sing., *Ann. Mycol.* **34**: 324. 1936

Type genus: Strobilomyces Berk.

Characters: Pileus fleshy, squamose to squarrose, or squamulose to glabrous, viscid, or not viscid, small to large, the margin frequently projecting; hymenophore tubulose, rarely lamellate, tubes usually comparatively long halfway between the margin and the stipe, strongly convex beneath, depressed to adnate, pores medium wide to rather wide when mature, discolorous or more frequently concolorous with the tubes; whitish to gray, or whitish to pale grayish cream color, becoming vinaceous pink to sordid purplish or yellow, golden yellow, the pores sometimes orange to red, at last olivaceous or yellowish brown, sometimes becoming black or red or blue on pressure; spore print black or nearly so, or, if not black, a very deep

brown with an olive tinge, or deep porphyry brown to reddish brown (« warm sepia », « hazel », « Sudan brown »), rarely (i. e. when tending to olive) approaching spore colors observed in the *Boletaceae*, e. gr. « Elk, Lama — » (Maerz & Paul) in *Boletellus pictiformis*, and then the spores differing microscopically from the latter; spores under the microscope richly colored when quite mature, fuscous to deep succineous melleous, with darker ornamentations (Pl. XXIV, 1-2, 4-10), more rarely persistently smooth (XXIV, 3), and then either remarkable for their large size (20-30 μ long), or for their comparatively thick walls (more than 1 μ in diameter), the endosporium usually interrupted at the apex forming an incomplete germ pore, or the apex applanate-truncate as in *Ganoderma*, or even more acuminate (Pl. XXIV, 3) than usual in the *Boletaceae*, globose, short-ellipsoid, subglobose, fusoid, rarely ovoid-fusoid; basidia and cystidia comparatively voluminous (Pl. XXIV, 1-3, 5-10), mostly more so than in species with comparatively equally long spores in the *Boletaceae*; hymenophoral trama strongly bilateral divergent of the *Boletus* subtype; stipe usually approximately cylindric and comparatively long and slender, smooth or ornamented with woolly or fibrillose scales, or with shallow to conspicuously projecting alveolate networks which in the most typical cases are waxy-slippery and bearing a hymenium; veil often present and then woolly or membranous, sometimes viscid, either fugacious, or persistent as an annulus on the stipe or as an appendiculate margin on the pileus, or both, never entirely glutinous, not yellow or green and pulverulent; stipe always destitute of glandulae: all hyphae without clamp connections. On earth, more rarely on the base of trees, or on decaying wood, most species preferring warmer climates, only two species reaching Canada, and only two known in Europe.

Limits : This family cannot be considered as artificial as it may appear to those who have studied only the species from certain local floras. It is not the ornamentation of the spores alone that characterizes this family. It is rather a large number of characters all characteristic for the family, not decisive if encountered isolated but always clearly defining the representatives of this family when occurring correlated with each other. These characters refer to the general habit (shape of the stipe, shape of the hymenophore), the spore print which unless it is olivaceous, never occurs in colors known in *Boletaceae*, the color and shape of the spores under the microscope, the thickness of the wall, the volume of the basidia and

cystidia and the surface markings of the stipe. They are often quantitative rather than qualitative, yet, with some experience, the mycologist soon learns to recognize a species of one of the three genera of the *Strobilomycetaceae* in the field, and, also learns to recognize a *Strobilomycetaceae* spore under the microscope, even if it is smooth. The strong network of some species of *Boletus*, e. gr. *B. Frostii* has often been compared with the alveolate surface of the stipe in species like *Porphyrellus subflavidus* or *Boletellus Russellii*. However, a closer examination of the two ornamentations will reveal that they are not identical. *B. Frostii* merely has an exaggerated reticulation of the *Boletus* type in the type subspecies, and a normal low one in ssp. *floridanus*. The *Strobilomycetaceae* with alveolate stipe, however, have a coarser, wide-meshed ornamentation which is covered with a different kind of hymenium. It cannot be denied that the two forms of network are homologous and represent nothing but the continuation of the hymenophore on the surface of the stipe, but this may also be said about the scabrosities of *Leccinum*, the glandulae of *Suillus*, and furfuraceous bodies on the stipe of some *Boleti* and *Xerocomi*.

It would be going too far if one would attempt to deny that the *Strobilomycetaceae* are related with the *Boletaceae*. But so are the *Paxillaceae*, and the *Gomphidiaceae*, yet, it has never been doubted that they belong in different families, or at least in different tribus (if what is called families in our present classification is still considered as tribus. In fact, the *Strobilomycetaceae* are not closer to the *Boletaceae* than the *Gomphidiaceae* or the *Paxillaceae*. The prejudice that all bolete-like fungi should be more closely related to each other than to « agarics » (i. e. to the lamellate *Agaricales*, has veiled the evidence. It is sufficient to remember the genus *Phylloporus*, a lamellate genus among tubulose genera, or *Filoboletus*, a tubulose genus among lamellate genera, in order to correct this opinion.

KEY TO THE GENERA

A. Spores globose to short ellipsoid; hymenophore white to gray at first, becoming darker in age; stipe not waxy costate-lacunose; pileus and stipe either warty or wooly or spinose squarrose ... 159. *Strobilomyces*

A. Fungi not combining these characters.

B. Tubes and pores in the young carpophores white to pale grayish cream color, becoming light pinkish vinaceous or sordid gray to porphyry brown with a grayish tinge when quite mature; spores with short cylindric spines imbedded in the episporium making the spores appear punctulate

when their upper surface is focussed upon (type XII), in some cases the vast majority or all spores smooth; print varying from « warm sepia » to « Sudan brown » (Ridgway) or « hazel » (Ridgway) or « Mohawk » (Maerz & Paul) without any olivaceous tinge . . . . 160. *Porphyrellus*

B. Tubes yellow in youth, becoming melleous or brownish melleous, or olivaceous with age; spores with an ornamentation as described above, or with longitudinal wings (type X), or else smooth (most frequently with longitudinal wings); spore print deep brownish olivaceous to black, not reddish when fresh. . . . 161. *Boletellus*

159. STROBILOMYCES Berk.

Decades Fungi, Hooker's Journ. Bot. **3**: 77. 1851.

Type species: S. strobilaceus (Scop. ex Fr.) Berk.

Syn. *Eriocorys* Quél., *Enchir.*, p. 163. 1886.

Characters: Pileus usually scaly; hymenophore at first pallid or grayish pallid; spores short (Q = 1 — 2), reticulate (Pl. XXIV, 2), or warty (Pl. XXIV, 6), or with longitudinal wings (Pl. XXIV, 8), or spores smooth (ornamentation types I, X, XI, or IX), practically black in print at least as long as not thoroughly dehydrated; basidia usually very voluminous (Pl. XXIV, 1-2, 6,8); cystidia hyaline to brown, usually voluminous; stipe not ventricose, more or less veiled.

Development of the carpophores: Hemiangiocarpous in *S. floccopus* according to Heim.

Area: Most common in the subtropical belt of America and Asia, one species in the temperate zone of Europe and Asia and North America, one more in temperate to subtropical North America, three in tropical West Africa.

Limits: The limits of this genus have been discussed at length in *Farlowia* **2**: 103-106. 1945. There is no need of repeating this discussion since the result obtained is adequately expressed in the key to the genera which can be followed without further comments; the genus *Strobilomyces* as it is delimited by the key is well separable and very natural.

State of knowledge: The species of *Strobilomyces* are comparatively well known. Five species are completely known (except, for some of them, the chemical color reactions); and four are known incompletely but sufficiently to make their generic position certain.

Practical importance: *S. floccopus* is edible but has little importance as food.

SPECIES

Sect. 1. **GENUINI** Sing. (1945). Spores either smooth or with imbedded short spines or warts, or with ridges or reticulations (Pl. XXIV, 1-2, 6).

Type species: S. floccopus (Vahl in Fl. Dan. ex Fr.) Karst.

S. floccopus (Vahl. in Fl. Dan. ex Fr.) Karst. [S. strobilaceus (Scop. ex Fr.) Berk.]; *S. confusus* Sing.; *S. velutipes* Cooke & Massee; *S. nigricans* Berk.; probably also *S. polypyramis* Hooker fil. apud. Berk., *S. montosus* Berk., and *S. echinatus* Beeli.

Sect. 2. **PTEROSPORI** Sing. (1945). Spores winged-ribbed from the hilar end to the apex (Pl. XXIV, 8).

Type species: S. pterosporus Sing.

S. pterosporus Sing.; *S. costatisporus* (Beeli) Gilbert, and probably another species from the Belgian Congo indicated by Gilbert; probably also *Boletus ater* Heim.

KEY TO THE SPECIES

All known species except those imperfectly known have been keyed out by Singer in a key published in *Farlowia* **2**: 108. 1945.

160. PORPHYRELLUS Gilbert

Les Bolets, p. 99. 1931, em.

Type species: Boletus porphyrosporus Fr.

Syn.: Phaeoporus Bat., *Bolets*, p. 11. 1908, non Schröter (1888).
Boletus subgenus *Porphyrosporus* Smotlacha, *Monogr. Česk. Hub.*, p. 31. 1911.

Characters. Hymenophore initially white to pale grayish cream color; spore print « Mohawk », plate 8, J 3, or « Caldera » (Maerz & Paul), or in Ridgway terms: « warm sepia », « Sudan brown », « hazel », without an olivaceous tinge; spores longer than 1.5 times their breadth, with short spines imbedded in the episporium and scarcely projecting (Pl. XXIV, 4-5), or smooth; stipe smooth (and then often velutinous) or grossly alveolate, or finely reticulate. On the soil.

Development of the carpophores: Unknown.

Area: Mostly in North America and Australasia, but one species almost circumpolar.

Limits : This genus is clearly separated from *Strobilomyces* by the shape and ornamentation of the spores, and from *Boletellus* by the color of the spore print and the absence of yellow pigment in the hymenophore and the context. As for the smooth spored species, they are so similar to those with ornamented spores that a generic separation is impossible. In a few of the carpophores examined, the author found, among hundreds of smooth spores, one or two ornamented spores. The spore print color of the species of *Porphyrellus* is different from that of the genus *Tylopilus* (*Boletaceae*; in this latter genus, the spore walls are thinner in an average, and the pores are smaller in mature hymenophores.

State of knowledge : Seven species are known at present. Five of these are known in all details essential for their taxonomic position.

Practical importance : One species is edible but not very valuable; the role played by the species of *Porphyrellus* in the mycorrhiza question is not yet quite clear.

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SPECIES

Sect. 1. **TRISTES** Sing. (1945). Pileus not bright colored; spores mostly smooth; context and surface strongly reacting with KOH, as far as known (reactions of *P. tristis* still unknown).

Type species : P. tristis Pat. & Baker.

P. tristis (Pat. & Baker) Sing. (Boletus, Pat. & Baker); *P. pseudoscaber* (Secr.) Sing. (Boletus, Secr.; Boletus porphyrosporus Fr.; Porphyrellus, Gilbert) with two subspecies, ssp. *typicus*, and ssp. *cyaneocinctus* Sing.; perhaps also *Boletus sordidus* Frost (unless conspecific with the preceding species).

Sect. 2. **GRACILES** Sing. (1945). Pileus bright colored (yellow, rarely faded to whitish or clay color, cinnamon, etc.): spores with short imbedded spines, punctulate when the upper surface is focussed upon; KOH (also acids) without intense action on context and surface (i. e. no color reactions).

Type species : P. gracilis (Peck) Sing.

P. gracilis (Peck) Sing. (Boletus, Peck; Tylopilus, Henn.); *P. subflavidus* (Murr.) Sing. (Tylopilus, Murr.; Boletellus, Snell); *P. malaccensis* (Pat. & Baker) Sing. (Phylloporus, Pat. & Baker); probably also *P. Cookei* (Sacc. & Syd.) Sing. (Boletus, Sacc. & Syd.; Bolet us

KEY TO THE SPECIES

See Singer, *Farlowia* **2** : 150. 1945 for a key to the species of section *Graciles*

161. BOLETELLUS Murr.

Mycologia **1** : 10. 1909, em.

Type species : B. ananas (Curt.) Murr.

Syn. *Boletogaster* Lohwag, *Beih. Botan. Centralbl.* **42** (2) : 274. 1926.
Frostiella Murr., *Mon. Contrib. Herb. Univ. Fla. Agr. Exp. Sta.* 1 : 5, p. 6. 1942 (nom. nud.)

Characters : Pileus scaly, or naked, dry or viscid ; hymenophore with yellow colors, sometimes with red pores ; spore print from deep olivaceous to practically black ; spores well colored under the microscope, either smooth (Pl. XXIV, 3), or with imbedded short spines (punctate from above), or most frequently winged or ridged from « pole » to « pole » (Pl. XXIV, 7, 9-10), also reticulate in some species, always elongate, except in one species with reticulate ornamentation. On the soil, rarely on the base of trees or on very decayed wood.

Development of the carpophores : Unknown, probably mostly either pseudoangiocarpous or hemiangiocarpous.

Area : North America, and tropics and subtropics of South and Central America, Oceania, Australia, Asia and Africa.

Limits : The limits separating this genus from the other two genera of the *Strobilomycetaceae* are now quite obvious and do not need any further explanation. The smooth spored species of *Boletellus* are sometimes confused with *Xerocomus* or *Boletus*. They differ from *Xerocomus* among other things by the truly bilateral hymenophoral trama. They differ from *Boletus* in external appearance which is rather that of *Xerocomus* than of *Boletus*, but there are several species in *Boletus* which have the habit of *Xerocomus*. These are concentrated in the section *Subpruinosi*. The *Subpruinosi* differ from *Boletellus* in the characters indicated in the key, p. 133 under letter « H 3 ». The same is valid for the genus *Pulveroboletus* and allied genera of the *Boletaceae*.

State of knowledge : Fifteen species are known to belong in this genus, and several more belong most probably in one of the sections now established within *Boletellus*. The fifteen known species have

been studied thoroughly, and for some of them, the chemical characters have been indicated.

Practical importance: Nothing is known about this subject.

SPECIES

Sect. 1. **ANANAE** Sing. (1945). Pileus pink, reddish russet carmine, at least partly pallescent in many species not viscid; spores winged longitudinally, never smooth; length of the majority of the spores when fully mature 17 µ or more.

Type species: B. ananas (Curt.) Murr.

B. ananas (Curt.) Murr. (Boletus, Curt.; Strobilomyces pallescens Cooke & Massee; Boletellus, Gilbert); *B. porphyreus* (Pat. & Baker) Gilbert (Strobilomyces, Pat. & Baker); *B. emodensis* (Berk.) Sing. (Boletus, Berk.; Strobilomyces annamiticus Pat.; Boletellus, Gilbert); *B. obscurecoccineus* (Hoehnel) Sing. (Boletus, Hoehnel); *B. cubensis* (Berk. & Curt.) Sing. (Boletus, Berk. & Curt.); probably also *Boletus lignatilis* Berk. & Curt. and *Boletus guadelupensis* Pat. unless identical with the preceding species; possibly also *Boletus squamatus* Berk.

Sect. 2. **MIRABILES** Sing. (1945). Spores strongly elongate, over 20 µ long, smooth; apex of the stipe with a rather indistinct to distinct reticulation, or most of the surface of the stipe with longitudinal veins which anastomose with each other, but never entirely smooth; margin of the pileus projecting.

Type species: Ceriomyces mirabilis Murr.

B. mirabilis (Murr.) Sing. (Ceriomyces, Murr.; Xerocomus, Sing. 1940); *B. projectellus* (Murr.) Sing. (Ceriomyces, Murr.; Boletus, Murr.).

Sect. 3. **RETISPORI** Sing. (1945). Spores short, reticulate.

Type species: B. retisporus (Pat. & Baker) Sing.

B. retisporus (Pat. & Baker) Sing. (Boletus, Pat. & Baker).

Sect. 4. **CHRYSENTEROIDEI** Sing. (1945). Spores with longitudinal wings, or smooth, and then smaller than 19 × 15 µ; pileus usually not pink or purple or carmine but rather yellow, fuscous, or chestnut to cinnamon in the well known species; veil little developed or none; pileus and stipe not viscid; stipe not waxy lacunose alveolate.

Type species: B. chrysenteroides (Snell) Snell.

B. pictiformis (Murr.) Murr. (Suillellus, Murr.) and var. *fallax* Sing.; *B. Linderi* Sing.; *B. chrysenteroides* (Snell) Snell (Boletus, Snell 1936); *B. turbinatus* (Snell) Sing. (Boletus, Snell); probably also *Boletus chrysenteron* Bull. sensu Coker & Beers, which might be identical with *B. turbinatus*, but is certainly different from *Boletus chrysenteron* Bull. ex Fr. sensu aut. Eur., and does not occur in Europe); also *B. subfraternus* (Coker & Beers) Sing. (Boletus, Coker & Beers).

Sect. 5. **IXOCEPHALI** Sing. (1945). Sterile surfaces of the carpophore more or less viscid; spores longitudinally winged; stipe not waxy-lacunose alveolate.

Type species: *B. singaporensis* (Pat. & Baker) Sing.

B. singaporensis (Pat. & Baker) Sing. (Boletopsis, Pat. & Baker); *B. jalapensis* (Murr.) Gilbert (Ceriomyces, Murr.).

Sect. 6. **DICTYOPODES** Sing. (1945). Pileus tomentose, not viscid or scarcely subviscid; spores longitudinally winged, elongate; stipe waxy lacunose and consequently coarsely reticulate or longitudinally lamellate.

Type species: *B. Russellii* (Frost) Gilbert.

B. Russellii (Frost) Gilbert (Boletus, Frost).

KEY TO THE SPECIES

See Singer, *Farlowia* **2**: 107, 122, 130. 1945.

GENERA INCOMPLETELY KNOWN

Phyllobolites Sing. *Ann. Myc.* **40**: 59. 1942. « Differs from the *Paxilli* especially in the ornamentation of the spores... Pileus apparently always red; spores ovoid...; stipe solid, central... » Singer. The type species is *P. miniatus* (Rick) Sing. (Paxillus, Rick). This species has not been found again in Brazil. Rick has twice sent material tentatively determined as *Paxillus miniatus*, but in one case it turned out to be *Paxillus panuoides*, and in the other case it was a very characteristic reddish species of *Pleurotus*, but in neither case did the material agree with the original account given by Rick. Rick himself admitted that the material was incorrectly determined, but the type could not be found; it seems to be lost. Under these circumstances, *Phyllobolites* remains doubtful. The author has refrained, from the

beginning, from ascribing this genus to any particular family. Since two species, now assigned to two genera of the *Paxillaceae*, *Linderomyces* and *Neopaxillus*, seem to be strikingly similar to the original *Phyllobolites*, one may prefer to regard *Phyllobolites* as a genus of the *Paxillaceae* but the main issue is that Rick's species, unfortunately chosen as the type species of *Phyllobolites*, is evidently a doubtful species with little chance for later clarification, and consequently the genus based on it must remain doubtful itself.

RUSSULACEAE Roze

Bull. Soc. Bot. Fr. **23**: 51. 1876 (nom. nud. ut Russulariées); *l. c.* p. 110; R. Maire, *Recherches*, p. 131. 1902 (ut Russulacées); Lotsy, *Vorträge*, p. 708. 1907.

Type genus : Russula Pers. ex Gray.

Syn. : Lactariaceae Gäumann, *Vergleich. Morph. Pilze*, p. 529. 1926.

Characters : Pileus and stipe usually fleshy, often vividly colored; cuticle varying in structure, often covered by a layer of velar origin, the cuticle proper consisting of up to three layers (epicutis, hypodermium, and subcutis), and beneath it often a subhypodermial layer present; hymenophore ordinarily lamellate; the lamellae either normally alternating with the lamellulae, or the latter few, and irregularly interspersed, or entirely absent, and then all lamellae equal, usually very brittle, free to decurrent, distant to crowded, thick to moderately thin, wedge-shaped; basidia normal, 4-spored, rarely 2-spored; true cystidia rarely present except on the edges of the lamellae (cheilocystidia); macrocystidia commonly present, but in some species replaced by another type of pseudocystidia : gloeocystidia; hymenophoral trama subregular to irregular, or intermixed, in *Russula* more often intermixed, with numerous spherocysts present (Pl. XIX, 5), in *Lactarius* more often without spherocysts; spore print white to deep ochraceous or pinkish cream [illegible]; spores under the microscope hyaline to yellowish, usually short globose to short-ellipsoid, more rarely ellipsoid-oblong, never quite smooth but always

[illegible] For the *Russulaceae* a special color chart has been devised in order to differentiate between the various spore colors ranging from pure white to a deep ochraceous. This can be found in Crawshay (1930). Further spore color citations (« A », « B », etc.) refer to his plate.

beset with an exosporial ornamentation which is strongly amyloid (containing amylon according to Locquin); ornamentation of type I (Pl. XIX, 2), II, III, IV, V, VI, VII, VIII, or exceptionally in a small minority of the spores of a print — IX; heterotropic, usually with a more or less distinct hilar spot; stipe usually central, solid or hollow, or stuffed, with annular veil or without veil (more often evelate), without pseudosclerotium, without pseudorrhiza; context white, or colored, often containing a latex, consisting of nests of sphaerocysts and connective hyphae (heteromerous), all these elements nonamyloid and without clamp connections; gloeo vessels, oleiferous hyphae, or laticiters always present. On the ground in woods, usually forming mycorrhiza, more rarely on decayed wood.

Limits: This family is divided from the other *Agaricales* by a very abrupt and wide hiatus. The question of delimitation does not arise.

Phylogeny: It is very difficult to say whether *Lactarius* or *Russula* is more primitive. All indications point to a « parallel » development of these two main branches of the family *Russulaceae*; the evolution has not been entirely analogous in the sense that the trends of evolution in each genus were the same at any level. Consequently, the sections of the two genera are not homologous.

The author believes that both genera have their ancestors in the group of *Gastromycetes* now often called *Astrogastraceae* (*Hydnangium carneum* and related species, *Arcangeliella*, *Elasmomyces*, etc.).

KEY TO THE GENERA

A. Latex absent; pigments mostly intracellular, very rarely membranal or intercellular; Wood's light and polarized light causing a certain degree of luminescence; trama of the lamellae usually with sphaerocysts in the half nearer the edge; lamellae equal or intermixed 162. *Russula*

A. Latex present (except for older, dry specimens), either forming droplets of watery or milky opaque consistency, or merely moistening the surface of freshly bruised tissue; pigment often only membranal, and intercellular pigment also occurring; trama of the lamellae mostly (except for certain primitive groups) not containing sphaerocysts, at least in the half closer to the edge; lamellae practically always intermixed 163. *Lactarius*

162. RUSSULA Pers. ex S. F. Gray

Nat. Arr. Brit. Pl. 1: 618. 1821

Type species: R. lutea (Hudson ex Fr.) Fr.

Syn.: *Omphalia* Pers. ex S. F. Gray, *l. c.*, p. 611.
Russulina Schroeter in Cohn, *Krypt.-Fl. Schlesien* 3 (1): 550. 1889
Lactarelis Earle, *Bull. N. Y. Bot. Gard.* 5: 409. 1909
Dixophyllum Earle, *l. c.*, p. 410
Omphalomyces Batt. ex Earle, *l. c.*, p. 410

Characters: Same as those of the family, but latex absent; see also key above.

Development of the carpophores: Gymnocarpous in some species, pseudoangiocarpous in others.

Area: Almost cosmopolitan, from the Arctic to the tropics and from sea level to the alpine zones.

Limits: The limits have been expressed in the key above. The delimitation is practically never difficult because the presence or absence of the latex is sufficiently sharp a character to rely upon in fresh material since it is always constant. However, in dried material, one is pressed for secondary, anatomical or external characters, and for physical and chemical means of differentiation between *Russula* and *Lactarius*. Even with dried material, there are only two groups of species where the two genera seem to « touch » each other, and that is the *Albati Plorantes* complex and the *Archaeinae Lactariopsis* complex. In both cases, secondary characters can be found *ad hoc* in order to distinguish herbarium specimens of these sections, e. gr. in the case of *R. delica*, one can rely on the presence of sphaerocysts in the lamellae.

State of knowledge: *Russula* belongs to the genera that are usually carefully avoided by the mycologists because of the difficulty of determination. However, this does not indicate that the taxonomy of *Russula* is poorly known. On the contrary, our present knowledge of *Russula* is very good, and the difficulties one encounters in the identification of specimens arise from the multitude of species all very similar to each other, and the sparsity of specialists to assist in the identification of specimens. It also arises from the somewhat tedious necessity of gathering numerous facts about the species before it is possible to find a name for it. In fact, a good fresh spore print must be at hand, and its color must be determined according to Crawshay's chart, all the chemical reactions must be known, some from fresh, some from dried material: all the anatomical characters of the cuticle of the pileus, the cortical layer of the stipe, and the hymenophore must be known. The establishment of some of these data requires experience with rather complicated microchemical manipulations and

practice in dying and the use of the microtome. And finally, when all these difficulties are overcome, the name is by no means established beyond a doubt because then begins the decision in favor of one of the several names which are usually available The unsettled situation regarding nomenclatorial problems in *Russula* (because each author of modern treatments follows his own preferences in names) has undoubtedly a deterrent effect on the non specialist who is inclined, — unjustly in this particular case — to conclude from the stage of nomenclature on the general stage of knowledge in *Russula*.

However, there is no genus in the *Agaricales* where more species have been studied anatomically and chemically, in addition to exact macroscopical descriptions available in world monographs (which, however, are somewhat predominantly concerned with European material); there is no genus where more type specimens and authentic material has been critically revised in the light of modern methods. There is no genus on which more effort has been spent by local and traveling specialists including such regions as China, Madagascar, Florida, North Africa, Altai, Caucasus, etc.

It is possible that the continued study of the pseudocystidia and dermatopseudocystidia will eventually reveal the presence of certain subtypes that might advantageously be used for the distinction of species and subsections. The pseudocystidia of *Russula polyphylla* and *R. mutabilis* stained throughout their interior a deep and rich blue when dyed with cresyl blue, and sulfoformol did not stain but rather left them hyaline or a pale yellow (in *R. polyphylla*). In contrast to this, sulfoformol stains the pseudocystidia of *R. emetica* deep brown, and cresyl blue does not stain the contents of these bodies. The latter have been called macrocystidia by Romagnesi, and the pseudocystidia of *R. polyphylla* are, according to the definition, gloeocystidia.

It is also possible that more chemical reactions will be discovered. But as a whole, the characters of *Russula* have been evaluated to a very high degree, and the distinction of species is not too difficult after enough experience has been accumulated, and all data are patiently collected.

As for the choice of the correct name, the author has, as in the other chapters of the present book, attempted to adhere to the International Rules more rigidly than ever, including the choice of the sectional and subsectional names, even in cases where this attitude may be criticized as not conformable to tradition. Friesian

names are admitted in a certain sense even if this interpretation cannot be proved as being correct, if no serious discrepancies in the opinions of the authors exist; and if they do exist, the name was adopted only if the dissenting author is believed to be wrong for some serious reason. As important and serious, the author considers such dissenting opinions as have been published by modern specialists of the genus or by authors whose views have greatly influenced the literature. Even so, the decision in certain cases cannot be considered as entirely due to nomenclatorial reasoning but must necessarily be partly based on the personal views of the author in regard to the reliability of certain data published in original descriptions, in regard to the probability of a certain interpretation in view of the occurrence of a species in certain regions and in view of the value attributed to published or unpublished pictures which are or are not in complete agreement with the diagnoses.

The author recognizes now 206 fully known species in the genus.

Practical importance : Russulas are used for food in many countries, especially by the Slavic population of Eastern Europe. Few species are valuable for anything else but pickling or salting. *R. cyanoxantha* is one of the exceptions. Nevertheless, *Russulae* are often found in the markets of Western Europe. Only one species is considered as probably slightly poisonous, viz. *R. foetens*.

Many *Russulae* are considered as a good source for certain enzymes, especially tyrosinase.

The majority of the *Russulae* occurring in the temperate zones must be considered as obligatory mycorrhizal fungi forming ectotrophic mycorrhiza with forest trees of various families, mostly conifers (*Pinus*, *Picea*, *Abies*, *Larix*, *Pseudotsuga*, *Tsuga*, etc.) and *Fagales* and *Salicales*, but they are also found to form mycorrhiza with *Tilia*. It seems that most of these species live normally under the conditions of mutual symbiosis; consequently they may become of some importance in forestry.

SPECIES

The author has attempted, during the years of special study devoted to the genus *Russula*, to improve gradually his own system of classification. This, in turn is the logical outgrowth of older classifications. Fries' classification must already be considered as approximately natural even though imperfect and incorrect in detail and

scope. Maire (1910) improved this classification considerably, and the more recent classifications are merely attemps to build upon this basis. The version of 1926 was strongly emended in 1932, again in 1942, and now again in the present survey. The most important changes are (1) the introduction of certain additional subsections, — a development dictated by the growing number of species, and (2) the transfer of the *Xerampelinae* to the *Rigidae*, according to a suggestion made by R. Heim in 1938; there are also some translocations between the *Rigidae* and the *Constantes* which are now called *Fragiles* Fr. em. because of priority reasons. In addition to this, some smaller changes were made which will allow us to define more clearly and sharply the limits of the sections and subsections. The new classification also attempts to express the best suggestions made by such recent students of the *Russulae* as Heim, Konrad & Josserand, Romagnesi.

As emphasized before, the classification is natural only insofar as the subsections are concerned. The sections are not all natural on the higher level, i. e. the farther away we move from the primitive *Russulae*, and especially in the *Fragiles*. The *Fragiles* may be terminal ramifications of several of the more primitive groups, but, it is here assumed, that for the most part, they are a continuation of the *Rigidae*.

Sect. 1. **PELLICULARIAE** Heim (1938). Fungi combining several primitive characters. (Choose this section if the development of the carpophores is pseudoangiocarpous, or the spores are nearly orthotropic (Pl. XIX, 2), or the stipe is attached to the substratum by a white disc or/and the margin is plicate grooved rather than sulcate-tuberculate; the spore print is here always white to pale cream; the color of the pileus is often very bright; cuticle with at least two well-defined layers; mycelium not forming mycorrhiza, at least not with conifers, *Fagales*, or *Salicales*; tropical and subtropical species from Africa and South America, perhaps also from Asia).

Type species: *R. annulata* Heim.

Subsection **Radicantes** Heim (1938). Context staining yellow; oxidase reaction weak according to Heim; annulus movable, sometimes fugacious, or adhering to pileus, or absent; stipe acuminate into a short pseudorrhiza; spores with rather isolated warts.

Type species: *R. radicans* Heim.

R. radicans Heim; perhaps also *R. xylophila* Beeli.

oxidase reaction weak; annulus none; stipe without a pseudorhiza; spores with more or less isolated warts.

R. aureotacta Heim.

Subsection Discopodinae Heim (1938). Context not deeply stained yellow at any age; oxidase reaction strong; annulus movable, sometimes fugacious, or adhering to the margin, or absent; stipe colored, not white; spores almost orthotropic (subsymmetric in relation to the axis) and practically globose, with a strongly raised network (ornamentation I-II); basal disc often present.

Type species: *R. annulata* Heim.

R. Puiggarii (Speg.) Sing. (R. brasiliensis Sing.); *R. annulata* Heim, with several varieties, forms and subspecies, among them the following species (probably specifically identical with *R. annulata* according to Heim): *R. annulatosquamosa* Beeli, *R. annulatolutea* Beeli, *R. annulatoangustifolia* Beeli, and *R. annulatobadia* Beeli.

Subsection Heliochrominae Heim (1938). As in the preceding subsection but constantly without annulus; spores strongly heterotropic and asymmetric, short-ellipsoid, with warts which are usually connected by very thin lines (ornamentation III-IV); basal disc none.

Type species: *R. heliochroma* Heim.

R. heliochroma Heim; *R. tricolor* Heim non Murr.; *R. Decaryi* Heim.

Sect. 2. COMPACTAE Fr (1938). (*Portentosae* Quél. 1886; *Lactarioideae* Bat. 1908; *Nigricantes* Konr. & Joss. 1934). Pigmentation fuliginous, gray, umber, rarely with a purplish or olivaceous tinge, or brownish tan to ochraceous tan, or else without any pigment; lamellae either extremely distant, or very numerous, or else moderately numerous, polydymous or not; basidia rather elongate; spores pure white to cream color, usually distinctly asymmetric heterotropic, rarely almost orthotropic symmetric; margin distinctly acute and smooth; cuticle often not distinctly divided into epicutis and hypodermium but often with an upper velar layer; reaction with $FeSO_4$ always distinctly positive, either pinkish gray to salmon, or green; number of spherocysts in the hymenophoral trama somewhat reduced in some groups; context extremely brittle to very hard and elastic, often changing on injury.

Type species: *R. nigricans* (Bull. ex) Fr.

Subsection Archaeinae Heim (1938). Context subfragile, some-

very distant, with or without irregularly intermixed lamellulae, not polydymous; surface of the pileus adorned with a warty velar layer, or without it; pileus never fuliginous or gray, and carpophores never blackening, habit of *Hygrophorus*.

Type species: *R. archaea* Heim

R. archaea Heim; *R. Hoehnelii* Sing.; *R. Earlei* Peck (R. Morgani Sacc. sensu Sing.); *R. fragilissima* Heim.

Subsection **Plorantes** Bat. (1908). (*Constantes* Lange 1926; *Delicinae* Melz & Zv. 1927). Context compact and hard when young, not brittle; lamellae very crowded to moderately close, with irregularly intermixed lamellulae, not truly polydymous; pileus never fuliginous or gray and carpophores not blackening; habit of *Lactarius*.

Type species: *R. delica* Fr.

R. delica Fr. (R. brevipes Peck; R. chloroides (Krombh.) Bres.); *R. pseudodelica* Lange; *R. vesicatoria* Burl.; *R. lilacipes* Shear; obviously also *R. delicula* Romagnesi (if different from *R. delica*).

Subsection **Nigricantes** Bat. (1908) (*Adustae* Lange 1926). Context compact and hard when young; lamellae distant to crowded, polydymous (mostly tridymous); surface smooth and glabrous excepting a tomentose margin in young caps; pileus whitish tending to fuliginous or gray, umber, etc., and the whole carpophore inside and outside tending to blacken in age, or by autoxidation.

Type species: *R. nigricans* (Bull. ex Fr.) Fr.

R. adustoides Heim; *R. robusta* Heim; *R. nigricans* (Bull. ex) Fr.; *R. latériticola* (Heim) Sing. (R. densifolia var. lateriticola Heim); *R. albonigroides* Sing.; *R. densifolia* (Secr.) Gillet; *R. adusta* (Pers. ex Fr.) Fr.; *R. albonigra* (Krombh.) Fr. (R. sordida Peck; R. subsordida Peck), probably also *R. purpureonigra* Petch.

Subsection **Rubentinae** Heim (1938). Differing from the preceding subsection in the context which becomes red rather than black in age, and the surface of the pileus which is finely tomentose woolly all over.

R. rubens Heim.

Subsection **Murinaceinae** Heim (1938). Differing from the *Nigricantes* in being grossly tomentose punctate, mouse gray.

R. murinacea Heim.

Sect. 3. **DECOLORANTES** (R. Maire 1910) Sing. (1926). Chemically close to the *Compactae* but anatomically and in the gross characters transient to the higher forms: Formalin strongly reacting with the fresh context; but pigments often bright colored, with well

developed epicutis and hypodermium, with non-polydymous lamellae, often with obtuse margin, with numerous spherocysts in the hymenophoral trama, and spore print often deeper colored than white or cream color (i. e. often deeper colored than « D »).

Type species : *R. decolorans* Fr.

R. consobrina (Fr. ex Fr.) Fr.; *R. magna* Beardslee: *R. subsericeonitens* Murr. (R. furcatifolia Murr.); *R. subdepallens* Peck; *R. nigrescentipes* Peck; *R. rubriceps* (Kauffm.) Sing.; *R. subobscura* Murr.; *R. rubescens* Beardslee [R. Kauffmaniana (Sing.) Sing.]; *R. vinosa* Lindbl. (R. decolorans var. obscura Romell); *R. occidentalis* (Sing.) Sing. (R. vinosa ssp. occidentalis Sing.); *R. seperina* Dupain; *R. flava* (Romell) Romell apud Lindblad (R. claroflava Grove sensu Melzer & Zvára, J. Schäffer, non Cooke; R. decolorans var. flava Romell; R. decolorans var. constans Karst. non Britz.); *R. cinerascens* Beardslee; *R. Burkei* Burl.; *R. Steinbachii* Cernohorsky & Sing.; *R. decolorans* Fr.; *R. subdensifolia* Murr. (R. subflava Sing.); obviously also *R. californiensis* Burl.

Sect. 4. **INGRATAE** Quél. (1888) em. R. Maire (1910), Heim (1938), non Melzer & Zvára (1927), J. Schaffer (1933). Pigment gray, brown, ochraceous, buff or melleous, lemon yellow, or greenish cream color, or else a combination of these colors, or absent over most of the surface of the carpophores; margin of the pileus usually more or less acute when young; taste often acrid; odor often fetid or pungent, or somehow specific but not fruity as in *R. emetica* and not spicy as in *R. maculata*; spore print white (A of Crawshay) to cream color (not darker than between C and D of Crawshay); rudiments of a veil often present; pileus often turning darker with KOH.

Type species : *R. foetens* Pers. ex Fr.

Subsection **Fistulosinae** Heim (1938). Velar rudiments consisting of scurfy areolate or punctate squamulose to granular, firmly attached coverings, made up of thick- or thin walled « empty » (not dermatopseudocystidioid) elements; pileus with a dry or humid non separable cuticle; spores with reticulate ornamentation, or more rarely echinate.

Type species : *R. fistulosa* Heim.

R. fistulosa Heim; *R. Balloui* Peck; *R. tennesseensis* Sing. (perhaps a variety of the preceding species); *R. liberiensis* Sing.; *R. crassotunicata* Sing.; *R. Burlinghamiae* Sing. (R. insignis Burl. non Quél.); *R. tuberculosa* Heim belongs either in this or in the following subsec-

Subsection **Obtectae** Sing. (1948). Velar rudiments consisting of an inconspicuous scurf or appresed squamulae or granular coverings which are rather firmly attached to the cuticle proper; the latter is easily separable at least in the marginal part of the pileus and more or less viscid in wet weather at least in the central half of the pileus; velar layer made up of thin walled, « empty » elements, spores with isolated spines or warts, or almost so.

Type species: R. obtecta Sing. (= *R. granulata* Peck).

R. granulata Peck (R. obtecta Sing.); probably also *R. affinis* Burl. and an undescribed species from Florida.

Subsection **Subvelatae** (Sing.) Sing. (sect. *Subvelatae* Sing. 1932). Velar rudiments consisting of loosely attached, friable, bright colored, arachnoid-pulverulent floccons the latter made up of thin filamentous or clavate hyphae, and strongly reacting with KOH.

Type species: R. subvelata Sing.

R. subvelata Sing.; *R. pulverulenta* Peck; *R. mutabilis* Murr.

Subsection **Foetentinae** Melzer & Zvára (1927) (*Foetentes* Konr. & Joss. 1935). No velar rudiments present; surface of the pileus stained darker by KOH; pileus in dull colors, or ochraceous, or pallid; odor of nitrobenzene, or oily, or of camembert cheese, of fish, of iodoform, of malt, etc.; margin of the pileus always pectinate-sulcate to tuberculate sulcate and distinctly subacute to acute.

Type species: R. foetens Pers. ex Fr.

Stirps **Farinipes** (Spore print nearly white: A).

R. farinipes Romell apud Britz. sensu Romell apud J. Schaffer.

Stirps **Foetens** (Pileus yellowish ochraceous-rusty brown, to rarely almost pallid; odor often of nitrobenzene, or similar).

R. foetens Pers. ex Fr.; *R. Laurocerasi* Melzer, *R. punctipes* Sing.; *R. deremensis* Henn.; *R. elastica* (Heim) Sing.; *R. ventricosipes* Peck; perhaps *R. consobrinoides* Heim. Also an undescribed species from Florida.

Stirps **Pectinata** (Pileus rarely colored as in stirps *Foetens*, but usually more grayish fuliginous, umber, bister, or pallid sordid; odor of camembert, or fresh fish, of iodoform, or malt, or spermatic).

R. pectinatoides Peck; *R. pectinata* Fr. sensu Sing.; *R. sororia* (Fr.) Romell (R. consobrina var. sororia Fr.); *R. periglypta* Berk. & Br. sensu Pat. is a species of this group or stirps *Farinipes*; *R. pallescens* Karst. is a pallid form of one of the species indicated above.

Subsection **Felleinae** Melz. & Zvára (1927). No velar layer present, and KOH not darkening the pigment of the pileus; pileus

sometimes rather vivid yellow, not gray, fuliginous, umber, but often white in the marginal portion in certain species; odor fruity as in *R. Queletii* (compote of pears), or mustard or soap flakes, more rarely absent.

Type species : R. fellea (Fr.) Fr.

Note : This subsection connects the *Ingratae* with the *Fragiles*, and might just as well be transferred to the *Fragiles*, in the immediate neighborhood of the *Emeticinae* and *Sardoninae*. It is indeed a question whether this would not make it easier to define the section *Ingratae* as well as the section *Fragiles*. But since there are also strong reasons in favor of keeping the *Foetentinae* and the *Felleinae* in one section, the author has decided in favor of the traditional solution.

R. fellea (Fr.) Fr. with ssp. *simillima* (Peck) Sing. (R. simillima Peck); *R. ochroleuca* Pers. ex Fr.; *R. citrinochlora* Sing.; *R. citrina* Gillet; *R. Raoultii* (Quel.) Sing. (R. ochroleuca var. Raoultii Quel.); *R. solaris* Ferdin. & Winge; *R. anomala* Peck (R. subalbidula Murr.); *R. innocua* (Sing.) Sing.; possibly also *R. alcalinicola* Burl.

Sect. 5. **RIGIDAE** Fr. (1838) (*Heterophyllae* Fr. 1851; *Lilaceae* Konr. & Joss. 1935). Pileus pruinate all over (not merely with a detersible and very fugacious pruina at the extreme margin), subvelutinous to velutinous, subtomentose to tomentose, areolate, squamulose rimulose, or scurfy to sericeous, more rarely glabrous; taste mild, bitter, moderately acrid in the young lamellae (and then margin at first somewhat acute), or strongly acrid (and then lamellae polydymous or regularly forked, or dermatopseudocystidia absent); formalin with context not reddening: $FeSO_4$ with context negative, or green, or salmon color, or grayish pink to pinkish gray-sordid (normal); spore print A, B, C, or D; cuticle of the pileus not darkening with KOH; context not becoming or staining yellow or yellowish brown unless it becomes olive green with $FeSO_4$.

Type species : R. lepida Fr.

Subsection **Elephantinae** Sing. (1932). Pileus brown, ochraceous brown, not green or purple; margin acute; cuticle glabrous to scurfy; lamellae neither polydymous nor the forked ones regularly intermixed; $FeSO_4$ strongly reacting (salmon color); spore print A to C; taste mild; context rather compact.

Type species : R. elephantina Fr.

R. elephantina Fr. (R. mustelina Fr.); perhaps *R. persobria* Sing. ¹ ².

Subsection **Cyanoxanthinae** Sing. (1932). Pigment nearly absent, or bright colored (violet, lilac, livid vinaceous, green, pinkish vinaceous, or often not abundant, and the pileus rather pale and somewhat multicolorous); cuticle glabrous, or sericeous, or scurfy; lamellae with numerous lamellulae or forked lamellae often interspersed in a more or less alternating manner, rather flexible and not brittle; $FeSO_4$ usually (unless spores oblong) almost negative with the context, or slightly grayish green; spore print A or B; margin of the pileus acute.

Type species: R. cyanoxantha (Schaeff. ex Schw.) Fr.

R. cyanoxantha (Schaeff. ex Schw.) Fr., var. *typica* (f. typica, f. Peltereaui Sing., f. lilacina Britz., f. pallida Sing.), var. *variata* (Bann. apud Peck) Sing. (R. variata Bann. apud Peck); *R. heterospora* Beardslee; *R. cremoricolor* Earle; *R. albiduliformis* Murr.; obviously also *R. cutefracta* Cooke sensu Romagnesi (unless conspecific with *R. cyanoxantha*).

Subsection **Schizoderminae** Sing. Pigment bright colored or dull; cuticle broken into small areolae, squamulose rimulose; epicutis devoid of gloeo-vessels, and macrocystidioid oleiferous hyphae, also devoid of spherocysts.

Type species: R. schizoderma Pat.

R. schizoderma Pat.; *R. septentrionalis* Sing.; *R. yunnanensis* Sing. with var. *pseudoviridella* Sing.

Subsection **Polyphyllinae** Sing. Pigment of the pileus almost none, or if present, green; a scurfy upper layer of the cuticle consisting mainly of gloeo-vessels or macrocystidioid oleiferous hyphae.

Type species: R. polyphylla Peck.

R. polyphylla Peck (R. magnifica Peck); *R. polycystis* Sing.; *R. viridella* Peck.

Subsection **Lividinae** Melzer & Zvára (1927). Pileus with bright colored pigment but not bright red; margin subacute, the cuticle often receding from the extreme margin leaving the latter denudate; context never reacting normally (pinkish gray-sordid) with $FeSO_4$ but either gray green in part, or salmon color, never negative; taste perfectly mild; context not turning yellow or brown on bruising, odor not of trimethylamin; spore print white (A, A B); epicutis (Pl. XVIII, 1) with ciliate dermatocystidia (not blue in sulfovanillin), or hair-like.

Type species: R. vesca Fr.

R. vesca Fr.; *R. furcata* (Gmelin ex Fr.). Fr. sensu Ricken [R. he-

terophylla (Fr.) Fr. sensu J. Schäffer]; *R. flocculosa* Burl.; *R. ferrotincta* Sing.; obviously also *R. rigida* Vel. (« R. livida Pers. » Melzer & Zvára, non Agaricus lividus Pers. ex Schwein., Secr.).

Subsection **Griseinae** J. Schäffer em. (1935). Pileus with bright colored pigment but neither bright rose red, nor yellow, with subacute to almost obtuse margin, the latter rarely denudate; context most frequently reacting normally (pinkish-gray sordid) with $FeSO_4$ but sometimes showing a more salmon reaction over part of the context, never negative or green; spore print B or C (C D), never A; epicutis usually with some dermatopseudocystidia, or at least potentially so, sometimes with numerous dermatopseudocystidia and ciliate dermatocystidia at the same time but then the latter without a subcuticular layer of noticeably shortened and partly subisodiametric elements (in the latter case, if there are no dermatopseudocystidia — see *Virescentinae*, and if there are dermatopseudocystidia — see *Amoeninae*); taste usually not perfectly mild in young specimens (hymenophore slightly acrid when quite fresh), never bitter; pileus somewhat scurfy, or pruinate, or velutinous, or glabrous.

Type species: *R. grisea* (Pers. ex Secr.) Fr. sensu Gillet (= *R. palumbina* Quél.).

R. palumbina Quél. [R. grisea (Pers. ex Secr. ut Agaricus) Fr. sensu Gillet, non Agaricus griseus Fr. 1821; R. furcata sensu Melzer & Zvára]; *R. ornaticeps* Burl.; *R. parazurea* J. Schäffer; *R. sublevispora* (Romagnesi) Romagnesi; *R. Ferreri* Sing.; *R. maxima* Burl.; probably also *R. anatina* Romagnesi (R. palumbina Quél. sensu Melzer & Zvára unless conspecific with R. Ferreri).

Subsection **Amoeninae** Sing. Pileus brightly colored (pink, brigth pink-red to red, purple to violet, green, lilac to almost black in the center, olive to partly brown, frequently bright yellow to dull yellow); stipe also either white or pink or purple or greenish or yellow; cuticle of the pileus and sometimes also the stipe with a characteristic bloom in dry weather; spore print A (then the taste not mild, either with a bitter component, or dermatopseudocystidia on pileus numerous), or B, C, or D; epicutis of the pileus consisting mainly of long hairs (piliform dermatocystidia) which also occur on the edge of the lamellae, or with a mixture of broadened subvesiculose terminal bodies and hair shaped dermatocystidia, or with a mixture of ciliate dermatocystidia, primordial hyphae, and normal (often incrusted) hyphae (then pileus yellow, and taste not mild), or else

ciliate dermatocystidium as terminal member (a structure intermediate between that of the *Lividinae* and the *Virescentinae*), and then with dermatopseudocystidia present; taste mild, or slightly acrid in young lamellae, or more or less acrid and bitter at the same time.

Type species: R. amoena Quél.

Stirps **Modesta** (Dermatopseudocystidia present on the pileus; spore print A or B, often with a more salmon tint than B; pileus and stipe not yellow).

R. leucomodesta Sing. ined. (Florida); *R. modesta* Peck; *R. Hibbardiae* Burl.

Stirps **Amoena** (Dermatocystidia absent; cheilocystidia usually « empty » and acute; spore ornamentation most frequently ridged, rarely reticulate; pileus and stipes sometimes yellow; spore print never pure white, sometimes reaching D, at least B).

R. Mariae Peck; *R. alachuana* Murr.; *R. amoena* Quél.; *R. tuberculata* Murr.; *R. variicolor* Murr.; *R. violeipes* Quél; *R. flavida* Frost & Peck apud Peck.

Stirps **Ochroleucoides** (Pseudocystidia of the gloeocystidial type; spore print A, A B; pileus and often stipe yellow).

R. ochroleucoides Kauffm. (R. dura Burl.).

Subsection Virescentinae Sing. (1932). Pileus with a more or less continuous covering (epicutis) that is similar and perphaps partly homologous with the velar layer of the *Fistulosinae*, soon breaking into areolate patches and furfuraceous particles, consisting of spherocysts most of which are mucronate as a piliform or ciliate dermatocystidium arises from its upper side, with or without a septum (this structure, the *Virescens* structure, is characteristic for this one subsection in *Russula* and for the section *Plinthogali* of *Lactarius*).

Type species: R. virescens (Schaeff. ex Zanted.) Fr.

R. chlorinosma Burl. (R. maculosa Murr.); *R. Patouillardii* Sing.; *R. virescens* (Schaeff. ex Zanted.) Fr.; *R. crustosa* Peck; *R. heterosporoides* Murr.

Subsection Lilaceinae Melz. & Zvára (1927). Pileus subglabrous, subvelutinous, or pruinose, bright colored, mostly blue to purple, red to pink, white, without dermatocystidia, usually with numerous primordial hyphae; margin of the pileus rounded-obtuse; $FeSO_4$ reacting normally; sulfovanillin reacting normally with the dried context of the stipe; spore print A to C.

Type species: R. lilacea Quél.

R. lilacea Quél., with var. *retispora* Sing. and var. *Melzeriana* Sing ; *R. azurea* Bres. ; *R. Zvarae* Melzer ; *R. lactea* (Pers. ex) Fr. ; *R. praeumbonata* Burl. ; *R. uncialis* Peck ; *R. subminutula* Sing. (R. lilacea var. emeticicolor J. Schaffer) ; *R. lepidiformis* Murr. ; *R. subinconstans* Murr. (R. inconstans Murr. non Burl.) ; *R. pulchra* Burl. ; also a Javanese species which may be *R. viscosa* Henn. ; also *R. Hixsonii* Murr., *R. subfloridana* Murr. and at least two white species : *R. cremea* (Murr.) Sing. (R. heterospora var. cremea Murr.) and *R. Westii* Murr.

Subsection **Roseinae** Sing. Differing from the preceding subsection in strong positive reaction with sulfovanillin.

Type species : R. rosea Quél.

R. rosea Quél. sensu Sing. (1926) (R. aurora Krombholz sensu Melzer & Zvára, Sing. 1932) with var. *minutula* (Vel.) Sing. (R. minutula Vel.) ; *R. albida* Peck.

Subsection **Lepidinae** Melzer & Zvára (1927). Pileus rather thick and firm, with subvelutinous to subtomentose cuticle which is beset with dermatopseudocystidia (or other bodies which turn blue in sulfovanillin) ; taste bitter or mild ; margin rounded-obtuse ; $FeSO_4$ and sulfovanillin reacting normally with the context ; pseudocystidia of the lamellae not bluing in sulfovanillin (only grayish hyaline), or bluing.

Type species : R. lepida Fr.

R. lepida Fr. ; *R. subtilis* Burl. ; *R. Peckii* Sing. ; *R. perplexa* Burl. ; *R. sericeonitens* Kauffm.

Subsection **Xerampelinae** [1] Sing. (1932) [*Luteogratae* subsect.

[1] These varieties are quite constant. They may be considered as subspecies (in the sense of mycoecotype) or as species, forming a stirps *Xerampelina*. The type variety is var. *quercetorum* Sing. ; other European species, subspecies, or varieties are *R. Barlae* Quél. sensu W. G. Smith ; *R. graveolens* Romell [R. xerampelina var. olivascens (Fr. p. p.) Zvára] ; *R. xerampelina* var. *pseudomelliolens* Sing. (R. melliolens sensu Crawshay) ; var. *Marthae* Sing. ; var. *elaeodes* Bres. (near the following variety) ; var. *rubra* (Britz.) Sing. (R. Linnaei Fr. sensu Ricken). The latter two varieties represent the European conifer race. In America, the forms corresponding to the type, are either brighter red (*R. leryana* Murr.) or with deeper (E) spore color (*R. squalida* Peck), a pale (C) spored form (*R. fucosa* Burl.) is not very rare in New England, and a bright purple form in oak woods in New York may be determined as *R. subvelutina* Peck the type of which has been lost at Albany. *R. Arnoldae* Murr. is a typical Florida race. The Asiatic forms known to the author, are almost the same as those observed in Europe, but west of the Rocky Mts., in North America, and also in Florida, more species or subspecies or varieties belonging to stirps *Xerampelina*

Viridantes Melz. & Zvára ex Konr. & Joss. 1935; group *Viridantes* (without definite rank) Melzer & Zvara 1927). Pileus whitish, brown or bright colored, with often rounded obtuse margin, subglabrous to subvelutinous, with or without dermatopseudocystidia; lamellae not polydymous and not regularly forked; taste mild, or bitter, or very slightly acrid in the young lamellae; odor often of trimethylamin; context most frequently distinctly staining yellow or brown, or becoming so when old or on drying; spore print from A to almost G, most frequently A, B, C, D, or E; $FeSO_4$ with context blue-green to olive green or gray green rarely brown (often in *R. fucosa*); spores often with very strongly echinate ornamentation (IV, VI).

Type species: R. xerampelina (Schaeff. ex Secr.) Fr.

R. xerampelina (Schaeff. ex Secr.) Fr.; with numerous varieties in Europe, Asia, and America; *R. pseudolepida* Sing.; *R. orcina* Sing.

Subsection **Pusillinae** Sing. Pileus rather thin and fragile; pileus bright red or rose color with transitions to yellowish ocher in one species, often pale colored in these colors; dermatopseudocystidia present; spore print from B C to D; $FeSO_4$ and sulfovanillin reacting normally with the context, pseudocystidia bluing in sulfovanillin.

Type species: R. pusilla Peck.

R. humidicola Burl.; *R. pusilla* Peck.

Note: Some species are said to have acrid taste, but the anatomical analysis shows that there are no dermatopseudocystidia. This is against the rule valid for at least the section *Fragiles*, where all species with distinctly acrid taste also have dermatopseudocystidia bluing in sulfovanillin. The author has not studied the African species involved but the only American species coming into this category, *R. corallina* Burl., seems to belong to the *Rigidae* where it may be the type of a special subsection. *R. Heimii* Sing. (R. velutipes Heim non Vel.) and *R. citrinipes* Heim may also enter this group.

R. cinerella Pat. is also a species of the section *Rigidae* but it is not quite clear whether it belongs to subsection *Lilaceinae*, or to some other, perhaps new subsection. Further investigations, also on *R. cinerea* Heim, may provide additional evidence.

Sect. 6. **FRAGILES** Fr. (1838) (*Firmae* Fr. 1838; *Alutaceae* R. Maire 1910; *Polychromae* R. Maire 1910; *Constantes* Sing. 1926; *Acrirubentes* Konr. & Joss. 1935; *Carnosotenues* Killermann 1936;

have been collected but have not been described except for some of them that were published (as independent species) by Murrill

Leucosporae Quél. 1888 [illegible]; *Xanthosporae* Quél. 1888) [illegible]. Pileus glabrous and viscid when wet, and not pruinate, scurfy, sericeous, subvelutinous, subtomentose, areolate, etc. (except sometimes pruinate on the extreme margin with a detersible, fugacious pruina), unless the spores in print are deeper colored than D, or the context is very acrid and the lamellae are not regularly intermixed or forked; in one species, the pileus is sometimes subsericeous-floccose but then the reaction with $FeSO_4$ is normal and the flesh becomes yellow in age; $FeSO_4$ always reacting normally with the context, or else merely somewhat more toward the salmon orange side, or toward the pink side (by partial suppression of the grayish sordid component), in some species, but reaction never negative or green; formalin negative; spore print from A to H.

Type species: R. lutea (Huds. ex Fr.) Fr.

I. *Series of subsections* with the spore print from B to C, and the taste acrid, or mild; context tending to stain yellow or brown; dermatopseudocystidia present or absent.

Subsection **Melliolentinae** Sing. (1932). Context with a tendency to become yellow or brown; spore print about B, more rarely reach-

[illegible] If *R. emetica* is accepted as the type species of this section, and the section itself is considered as such rather than as a combination of sections under a heading without definite rank, then, and only then, the *Leucosporae* become a synonym of the *Fragiles*. If the *Constantes* are excluded from the *Leucosporae* as they were by Lange's 1926 emendation, the selection of *R. emetica* becomes logical. However, the author tends to the opinion that both the *Leucosporae* and the *Xanthosporae* of Quélet are not actually intended to be sections but rather « headings » for the next-following divisions which are here considered as sections. Consequently, the section *Piperinae* Quél. 1888 also becomes a synonym of the *Fragiles*; sect. *Ingratae* has been taken up by R. Maire for the section 4 of this survey; sect. *Sapidae* would be another synonym of section *Rigidae* Fr.

[illegible] *R. lutea* is assumed to be the lectotype of this group. The author doubts, however, whether it is correct to consider the *Xanthosporae* as a section, and tends to the opinion that they are merely a common heading for what is actually meant to be the sections, i.e. the *Tenellae*, *Insidiosae*, and *Versicolores* Quél. 1888. If this view is accepted — and it would be desirable to accept it not merely as being in accord with the spirit of Quélet's treatment but also in order to avoid the introduction of thus far neglected subsectional names —, the *Tenellae* would be typified, according to the proposal of the author, with *R. lutea* as the lectotype, and would become another synonym of the *Fragiles*, the *Insidiosae* should be considered based on *R. maculata* Quél., and thus become another synonym of the *Fragiles*, and the *Versicolores* should be based on *R. olivacea*, whereby they

ing C; stipe rather stout and usually not longer than the diameter of the pileus.

Type species: R. mellioleus Quél.

R. brunneoviolacea Crawshay (R. pseudoviolacea Joachim.; *R. mellioleus* Quél.; *R. viscida* Kudrna; perhaps also *R. purpurascens* Bres. (if different from the preceding forms).

Subsection **Puellarinae** Sing. (1932). Context with a tendency to become yellow ocher; spore print about C; stipe rather slender and fragile, usually longer than the diameter of the pileus.

Type species: R. puellaris Fr.

R. puellaris Fr.; *R. caucasica* (Sing.) Sing. (R. puellaris var. caucasica Sing.); *R. appalachiensis* Sing. (R. puellaris sensu Beardslee); *R. puellula* J. Schaffer & Moller; *R. microspora* Sing.

II. *Series of subsections* (*Fragiles* sensu Heim) with the spore print between A and E, taste always very acrid; dermatopseudocystidia very numerous.

Subsection **Emeticinae** Melzer & Zvára (1927) (*Acrirubentes* subsect. *Emeticae* Konr. & Joss.). Spore print A or B, rarely reaching C (scarcely in fresh spore prints), usually A or A-B, and if darker, spores with ornamentation VII, or at least fungi not corresponding to the diagnosis of the subsequent subsections.

Type species R. emetica (Schaeff. ex Fr.) Pers. ex Fr.

Stirps **Atropurpurea** (ornamentation of the spores usually very short (type VII), or else spore print B (C); pigment of the cuticle of the pileus in globules according to R. Maire, usually dark purple; margin obtuse).

R. atropurpurea (Krombholz) Britz. [with several subspecies and forms, the most important ones: ssp. *atropurpureoides* (Sing.) Sing. (var., Singer: the most common race in Western Europe); ssp. *atropurpurella* (Sing.) Sing. (var., Sing.); ssp. *rubripes* (var., Sing.); ssp. *Krombholzii* (Sing.) Sing. (var., Sing.); ssp. *Bresadolae* (Schulzer) Sing. (R. Bresadolae Schulz.)]; *R. rinacea* Burl.; *R. arenaria* Sing.

This stirps is close to subsection *Mellioleutinae* (*R. mellioleus* and *R. viscida*).

Stirps **Emetica** (ornamentation normally long, i. e. 0.4-1.5 µ; pigment variable, probably not in globules; spore print A or A-B, rarely reaching B).

R. emetica (Schaeff. ex Fr.) Pers. ex S. F. Gray, with several subspecies and forms, the most important ones: ssp. *euemetica* Sing.; ssp. *Mairei* (Sing.) Romagnesi (R. Mairei Sing.); ssp. *lacustris* Sing.;

ssp. *aquosa* (Leclair) Sing.; ssp. *fragilis* (Pers. ex Fr.) Sing [R. fragilis (Pers. ex Fr.) Fr.]; ssp. *alpestris* (Boudier) Sing.; ssp. *Alni jorullensis* Sing.

This stirps, consisting of a single species, was split into a series of species (in recent papers by Heim and by Romagnesi), mainly at the expense of what is here called ssp. *fragilis*. However, the author had no opportunity to form his own opinion on this new development.

Subsection **Sardoninae** Sing. (1932). Spore print B, rarely C; pileus usually purple, rarely greenish or melleous; margin of the pileus acute or subacute, or at first so, or becoming so; stipe usually pink to purplish pink or purple, rarely white, and if so, turning pink with ammonia.

Type species: R. chrysodacryon Sing.

R. fallax (Fr.) Sacc. sensu Sing.; *R. Queletii* Fr. apud Quél.; *R. chrysodacryoides* Sing.; *R. chrysodacryon* Sing. (R. sardonia Fr. sensu Lindblad, J. Schaffer; R. drymeia Cooke ex ic.); *R. altaica* (Sing.) Sing. (R. gracilis ssp. altaica Sing.); *R. gracilis* Burl. (R. gracillima J. Schäffer).

Subsection **Sanguininae** Melzer & Zvára (1927) (*Acrorubentes* subsect. *Sanguineae* Konr. & Joss. 1935). Spore print rarely A (and then surface staining bright and rich yellow where injured), or B, C, D, or E, most frequently D and D to E; pileus often bright red to carmine, at least on the margin, often with fuscous, blackish, rufous, or olive shades in the center, or else without any pigment; if pinkish-red or bright red (unicolorously), the cuticle is often little differentiated, especially in consistency and therefore hardly separable and the context beneath it reddens after prolonged exposure; margin of the pileus acute to subacute, sometimes becoming obtuse in age; context not turning pink with NH_4OH.

Type species: R. sanguinea (Bull. ex Poll.) Fr.

R. rosacea (Pers. p. p. ex) S. F. Gray em. Fr. [R. sanguinea (Bull. ex Pollini, non Wulfen ex Fr.) Fr.][1]; *R. rubicunda* Quél. sensu Bataille (R. subpunctata Kauffm.; R. Fosteriana Murr.); *R. luteotacta* Rea (perhaps rather to subsection *Emeticinae* but probably same as *R. mexicana* Burl.); *R. rhodopoda* Zvára; *R. Robinsoniae* Burl.; *R. americana* (Sing.) Sing. (R. rosacea var. americana Sing.); *R. helo-*

[1] Pollini's revalidation is at the same time a later homonym of *Agaricus (Cortinarius) sanguineus*, and Fries had therefore no right to take this name up

des Melzer; *R. pulchella* Borszczow [R. palustris Peck: R. exalbicans Melzer vix Agaricus exalbicans Secr.; R. depallens (Pers. ex) Fr. sensu J. Schaffer]; probably *R. albidula* Peck.

III. *Series of subsections* with the spore print from D to E (F), the taste mild or somewhat acrid in the young lamellae; context rarely tending to become yellow-melleous in the base; dermatopseudocystidia most frequently present, but often small and inconspicuous, rather rarely absent.

Subsection Subcompactinae Sing. (1932). Pigment of the pileus green, or somehow livid, or a mixture of these colors and at times some rusty spots, or some yellowish or pinkish mixed in, in other forms without any pigment; stipe usually rather stout and not much longer, more often shorter than the diameter of the pileus, not reddish.

Type species: R. subcompacta Britz. sensu Sing.

R. subcompacta Britz. sensu Sing.; *R. aeruginea* Lindblad apud Fr. (R. graminicolor Quel., vix Agaricus graminicolor Secr.); *R. basifurcata* Peck; perhaps also *R. alcalinicola* Burl. (but see *Ingratae*).

Note: This section is somewhat intermediate between the *Rigidae-Griseinae* from which it derives and the following section to which it seems to be close. *R. pulchella* f. *decolorata* is often extremely similar to *R. aeruginea* and *R. citrinchlora*.

Subsection Sphagnophilae Sing. Pigment of pileus sometimes green in rare forms, but mostly purple, brown, ochraceous tan, pinkish, red, often with very dark center, sometimes turning entirely green on drying; stipe usually not stout, and often longer than the diameter of the pileus and fragile, white or reddish; pileus with dermatopseudocystidia.

Type species: R. sphagnophila Kauffm.

R. disparilis Burl.; *R. Blackfordiae* Peck (R. serotina sensu Melzer & Zvara; R. versicolor J. Schaffer); *R. sphagnophila* Kauffm. (R. venosa Vel. sensu Melzer apud J. Schaffer); *R. cristulispora* Sing. [R. intensior (Cooke ?) Romagnesi]; *R. zonatula* J. Schaffer & Moller; *R. placita* Burl. sensu Sing. (1947) (R. sphagnophila var. heterosperma Sing.); *R. Zelleri* Burl.

Subsection Integrae R. Maire (1910). Pigment of pileus often bright red, also more yellow, or even avellaneous, reddish brown, fulvous, bay, etc., but not livid or green and not multicolorous-pallid; stipe usually not stout but also not elongate, i. e. not longer

except in very old carpophores, white to reddish; pileus with dermatopseudocystidia, more rarely without them.

Type species : R. paludosa Britz.

R. amygdaloides Kauffm. (? R. betulina Burl. sensu Kauffm. non Burl.; nec Melzer); *R. integra* (L. ex Vitt. p. p.) Fr. sensu Sing. (R. Velenovskyi Melzer & Zvára); *R. fusca* Quél. sensu Sing. (probably also Barbier) [R. integra var. fusca (Quél.) Quél.]; *R. cremeoavellanea* Sing.; *R. Font Queri* Sing.; *R. paludosa* Britz. [R. elatior Lindblad; R. rubrotincta (Peck) Burl.]; *R. lutensis* Romagnesi; *R. Melzeri* Zvára; *R. luteobasis* Peck [14]; *R. flaviceps* Peck sensu Burl.; *R. Beardsleei* Burl.

IV. *Series of subsections* (*Russulinae* in the sense of Singer 1926) with the spore print (C D to E) F, F G, G or H; taste mild, moderately acrid, strongly acrid, or bitter; context rarely tending to become yellowish, rather sometimes yellow from the start, or tending to become palest cinereous in the base; dermatopseudocystidia either present or absent.

Subsection Alutaceinae Melz. & Zvara 1927 (*Olivaceinae* Sing. 1932). Spore print G, or F, or in between these tones, or H; dermatopseudocystidia none; taste mild or nearly so.

Type species : R. alutacea (Pers. ex Schweinitz) Fr. sensu Melzer & Zvára [= *R. olivacea* (Schaeff. ex Secr.) Fr. vel. aff.].

Note : This subsection is probably merely a « projection » of the *Rigidae*, mainly *Lilaceinae*, into the *Fragiles*, having deep colored spores.

Stirps **Punctata** (Macrocystidia blue in sulfovanillin on the tip only; context with phenol normally reacting, i. e. becoming chocolate; odor usually like iodoform; pileus with a pruinose bloom; mycorrhiza with conifers; stature small to medium).

R. Murrillii Burl.; *R. Dadmunii* Sing.; *R. punctata* Krombholz sensu Sing. (R. Turci Bres. sensu R. Maire; R. amethystina Quél sensu J. Schaffer; R. chamaeleontina Fr. sensu Zvára).

Stirps **Lutea** (Macrocystidia bluing in sulfovanillin at the apex or more; context with phenol reacting normally; odor never like iodoform; pileus with a slight pruinose bloom, or opaque, or glabrous and somewhat shining; mycorrhiza with conifers or with frondose trees; stature small to large; context mild, not bitter)

[14] The exact color of the spore print has never been established; consequently, the final position of this species is still somewhat doubtful; it may be rather among the *Chamaeleontinae*, or some other place in the classification

R. neglecta Sing. (R. Turci Bres. p. p.); *R. Postiana* Romell (R. mollis Quél. sensu Romagnesi); *R. roseipes* (Secr.) Bres.; *R. lutea* (Huds. ex Fr.) S. F. Gray; *R. aurata* (With. ex) Fr.; *R. Romellii* R. Maire; *R. subalutacea* Burl. Obviously also *R. curtipes* J. Schaffer (unless conspecific with *R. Romellii*).

Stirps **Olivacea** (Cheilocystidia differentiated; context with phenol deep purple, never chocolate; odor not like iodoform; pileus subvelutinous, very opaque, large and thick; mycorrhiza with conifers and with frondose trees; context mild, not bitter)

R. olivacea (Schaeff. ex Schw.) Fr.

Stirps **Pseudointegra** (Macrocystidia incrusted; context with phenol becoming chocolate; surface of the stipe with sulfovanillin becoming bright red for a few minutes; spore print about F or F to G; taste bitter; cuticle with a bright red pigment; mycorrhiza with frondose trees).

R. pseudointegra Arnould & Goris.

Stirps **Amoenata** (Pileus shining, deep purple, more rarely pale pinkish red; surface of the stipe with sulfovanillin becoming bright red for a few minutes; spore print about F or F G; taste bitter in the cuticle of most specimens, the pileus often umbonate; mycorrhiza with conifers).

R. amoenata Britz.

Subsection Rubrinae Melzer & Zvára (1927), sensu str. Sing. (1932). Spore print E. or sometimes between E, F and G; taste extremely acrid; dermatopseudocystidia large and numerous; cuticle of the pileus strikingly opaque, rapidly drying, and often with a slight bloom, or scurf, or subvelutinous.

Type species: R. rubra (Fr. sensu Krombh.) Fr.

R. rubra Fr. sensu Bres. (non Agaricus ruber aut. prae-Fries. et Fr. 1821; *R. pungens* Beardslee; *R. Kavinae* Melzer & Zvára; *R. Handelii* Sing. — all probably geographic races of R. rubra); *R. badia* Quél.; *R. tenuiceps* Kauffm.

Subsection Chamaeleontinae Sing (1932). Spore print G, or H; cystidia strongly bluing in sulfovanillin; dermatopseudocystidia present; taste mild.

Type species: R. olivascens Pers. sensu Bres., sensu Singer, 1932, non 1935, non J. Schäffer, 1933 1934.

R. polychroma Sing. [R. alutacea ssp. integra Sing.; R. integra (L. ex Vitt.) Fr. sensu R. Maire, Melzer & Zvára, J. Schäffer, Moreau, non (L. ex Vitt.) Fr.]; *R. olivascens* Pers. ex (Schw.) sensu Bres.; *R.*

cessans Pearson (R. Turci Bres. p. p. sensu Sing. 1932); *R. chamaeleon* Sing.; *R. laeta* J. Schaffer & Möller; perhaps also: *R. aurantiaca* (J. Schaffer) J. Schäffer (sensu Romagnesi), *R. gilva* Melzer, *R. betulina* Burl. sensu orig., *R. alutacea* ssp. *ambigua* Sing.

Subsection **Urentes** R. Maire 1910 (*Urentinae* Sing. 1932; *Acrirubentes* subsect. *Maculatae* Konr. & Joss. 1935). Spore print G, or H, rarely between E and G with a tinge of F; taste acrid (often only slightly so); dermatopseudocystidia (Pl. XV, 1) present on pileus though sometimes little differentiated or thin but distinctly bluing in sulfovanillin.

Type species: R. urens Romell.

R. nauseosa (Pers. ex Schw.) Fr. (R. chamaeleontina Fr. sensu Lange, Sing.); *R. Allescheri* Sing. (R. nauseosa var. atropurpurea All.); *R. nitida* (Pers. ex Schw.) Fr. sensu Melzer & Zvara, Sing., J. Schaffer (R. firmula J. Sch.); *R. Cernohorskyi* Sing.; *R. atroviolacea* Burl.; *R. mesospora* Sing.; *R. Lundellii* Sing. (R. pulcherrima J. Schäffer); *R. Schiffneri* Sing. (R. veternosa Fr. sensu J. Schäffer); *R. aurantiolutea* Kauffm.; *R. maculata* Quél. apud Roze; *R. Bresadoliana* Sing. (R. veternosa Fr. sensu Bres.); *R. luteoviridans* Martin sensu Romagnesi; *R. pseudoemetica* (Secr.) Sing. sensu Sing. non Killermann; *R. macropoda* Sing.; *R. diaboli* Sing.; probably also *R. rutila* Romagnesi.; obviously also *R. urens* Romell apud Maire ex Sing.

KEY TO THE SPECIES

Keys are available, but they cannot be recommended except for small regions. The composition of a key to all species of *Russula* is a major undertaking, and since it is not in line with the primary subject of this book, viz. generic taxonomy, the author postponed the publication of a key to the *Russulae*.

163. **LACTARIUS** (D. C. ex) S. F. Gray

Nat. Arr. Brit. Pl. **1**: 623, 1821.

Type species: L. deliciosus (L. ex Fr.) S. F. Gray.

Syn.: *Galorrheus* (Fr.) Fr., *Syst. Orb. Veget.* p. 75. 1825; *Stirpes Agri. Femis.* **3**: 56. 1825.

Agaricus tribus *Galorrheus* Fr., *Syst. Mycol.* **1**: 61. 1821.

Lactifluus Roussel ex O. Kuntze, *Rev. Gen. Pl.* **2**: 856. 1891.

Lactaria Pers. ex Schroter in Cohn, *Krypt. fl. Schlesien, Pilze* **3**: 534. 1889.

Lactariella Schroter in Cohn, *l. c.*, p. 544.

Hypophyllum Paulet ex Earle, *Bull. N. Y. Bot. Gard.* 5: 408. 1909.
Gloeocybe Earle, *l. c.*, p. 409.

Characters: Pileus and stipe usually fleshy, often vividly colored; cuticle varying in structure; hymenophore ordinarily lamellate; the lamellae usually alternating with the lamellae (lamellae polydymous), moderately brittle, or not brittle at all, subdecurrent to decurrent, distant to crowded, thick to moderately thin, wedge shaped (Pl. XX, 1); basidia normal, 4-spored, rarely 2-spored; true cystidia sometimes present and then often thick-walled (Pl. XX, 1); cheilocystidia sometimes present; macrocystidia commonly present, more rarely absent; hymenophoral trama subregular to subirregular and intermixed with laticiferous hyphae (Pl. XX, 1) and in very few cases also with spherocysts (*Lactariopsis*); spore print white to deep ochraceous or pinkish cream; spores under the microscope as in *Russula* but ornamentations from I-III are more frequent than in *Russula*; stipe usually central, more rarely eccentric or lateral, veiled, or more often without a veil; pigments present all through the carpophore (not merely in the cuticle of the pileus), more rarely absent in the lamellae or the stipe, often membranal or intercellular and, in many species, at the same time also intracellular; context with latex (except for older, dry specimens), either forming droplets of latex which may be watery or milky, or merely moistened from the colored, milky latex; Wood's light and polarized light causing little luminescence in most species; laticiferous hyphae running through the tissue, very striking (Pl. XX, 1; XVIII, 5). On the ground in woods, usually forming mycorrhiza, more rarely on decayed wood.

Development of the carpophores: Some species are pseudoangiocarpous; others are gymnocarpous.

Area: Practically cosmopolitan.

Limits: See *Russula*, p. 699. Other genera with latex are: *Lactocollybia*, *Mycena*, *Rhodophyllus*, *Bertrandia*, and one form of *Termitomyces*.

State of knowledge: The genus *Lactarius* is comparatively well known. Most of the species have not been studied as thoroughly from all points of view as those of *Russula*, but there are usually more macroscopical characters on which the species concept can be based than there are in *Russula*. The number of species admitted in the following survey is 75.

Practical importance: *Lactarii* are used for food in many countries, especially *L. deliciosus* and *L. sanguifluus* in Europe and Asia, also

in North Africa. Enormous quantities of these species are annually sold in the markets of Barcelona, and other Catalonian cities. *L. resimus* and *L. scrobiculatus* are highest priced in Russia, where they are mostly salted (like sauerkraut) or pickled to be consumed with sour cream and vodka. However, all other *Lactarii*, including *L. torminosus* and *L. piperatus* are also used for the same purpose. *L. torminosus* is also used fresh. The only species that seems to be poisonous is *L. pallidus*, but it is doubtful whether only in cooked form, or also in pickled form. Edible species of a very different flavor are those *Lactarii* that are here united in the section *Dulces*. The only one occurring in Europe, *L. volemus*, is frequently sold in the markets.

Species of the genus *Lactarius* are a good source for various raw materials for drug production but since no practical means for cultivation of the fruiting bodies has been worked out, and the supply must be based on the carpophores gathered in the woods, it is unlikely that the *Lactarii* become industrially important.

As mycorrhizal fungi, the *Lactarii* may yet become important in forestry. Some species form mycorrhiza with conifers, others with frondose trees, mainly of the orders *Salicales* and *Fagales*.

SPECIES

Sect. 1. LACTARIOPSIDEI Sing. (1942). Pileus with a persistent pilose tomentose covering which consists of thick walled hairs; stipe frequently annulate or otherwise veiled, more rarely developing gymnocarpously and then differing from most other *Lactarii* in having an almost or quite heteromerous hymenophoral trama; pseudocystidia on the sides of the lamellae numerous and voluminous; spores with medium sized ornamentation (which does not correspond to the type I and to the type VI), ovoid subellipsoid (neither globose nor suborthotropic); context brittle; lignicolous, or on humus rich in woody matter. Tropical African species.

Type species : L. Zenkeri (Henn.) Sing.

Note : This section is close to the *Compactae*, subsection *Archaeinae* of *Russula*.

L. Zenkeri (Henn.) Sing.: *L. Pandani* Heim; *L. gymnocarpus* Heim apud Sing.

uppermost covering layer consisting of an epicutis of thin-walled elements; a « general » veil present; hymenophoral trama filamentous; pseudocystidia present on the sides of the lamellae; spores nearly globose and subsymmetric-suborthotropic, with a very high ornamentation of type I; context rather tough; lignicolous, or on humus rich in woody matter. Tropical African species.

L. adhaerens Heim

Sect. 3. **DULCES** Heim (*nom. subnud. ad. int.*) ex Sing. (1942). Taste completely mild except in one Brazilian species; pileus completely dry; latex extremely and strikingly abundant, unchanging or changing on exposure; cystidia either absent or present, and then not similar to the common pseudocystidia; spores either heterotropic or suborthotropic; cuticle often with an epicutis consisting of a palisade of dermatocystidia (not dermatopseudocystidia) and never with « Virescens structure » (Pl. XX, 1).

Type species: L. volemus (Fr.) Fr.

Subsection **Fulgentes** Heim (1938). Spores suborthotropic.

L. fulgens Heim.

Subsection **Rubroviolascentini** Sing. (1942). Spores heterotropic; latex almost transparent, pale reddish gray; cystidia often more or less thick walled.

Type species: L. rubroviolascens Heim.

Note: This subsection is somewhat intermediate between this section and the following section, in the color of the latex as well as in the structure of the cuticle. The latter consists of thick walled hyphae which immediately or mediately arise from sphaerocysts or sphaerocystoid hyphae in a deeper layer (in *L. Russula*). *L. Russula* is also somewhat aberrant in this section because of the acrid taste. It may yet be necessary to transfer the *Rubroviolascentini* to the *Plinthogali*.

L. rubroviolascens Heim; *L. Russula* Rick.

Subsection **Lactiflluini** (Burl. as « group » subdividing section *Russularia*) Sing (1942). Latex staining brown or unchanging but always initially white or seriflluous white, not watery transparent; spores heterotropic; thick walled cystidia present or absent.

Type species: L. volemus (Fr.) Fr.

L. pseudovolemus Heim; *L. hygrophoroides* Berk. & Curt. (*L. distans* Peck); *L. volemus* (Fr.) Fr.; *L. allochrous* Sing.; *L. purgatorii* Sing.; *L. luteolus* Peck; perhaps *L. Clarkei* Cleland.

Sect. 4. **PLINTHOGALI** (Burl. ut « Group » in *Russularius*) Sing.

(1942). Cuticle with distinct Virescens structure (Pl. XVIII, 4 5), velutinous to subglabrous-subvelutinous, variously colored, often white, or gray, or avellaneous-umber, or deep warm sepia to almost black; dry; latex milky white, or colored, or watery, and then colored, often white and then reddening, but also persistently white, or staining deep violet.

Type species: L. lignyotus (Fr. ex Fr.) Fr.

Subsection **Fuliginosi** (Konr. 1935 ut « groupe » subsectionis *Coloratorum*) Sing. Latex milky, not yellow.

Type species: L. fuliginosus (Fr. ex Fr.) (Fr. ex Fr.)

L. Gerardii Peck; *L. lignyotus* Fr.; *L. nigroviolascens* Atk.; *L. fuliginosus* (Fr. ex Fr.) Fr. (with three subspecies); *L. sublatus* (Murr.) Sing. (Melanoleuca, Murr.).

Subsection **Xanthydrorheini** Sing. Latex watery, yellow.

L. xanthydrorheus Sing.

Sect. 5. **ALBATI** (Bat.) Sing. 1942 (*Velutini* subsect. *Albati* Bat. 1908). Pileus dry, practically pigmentless; latex white or whitish, unchanging or more often somewhat changing on exposure, acrid (or at least context acrid); spores heterotropic; cuticle not showing any trace of Virescens structure.

Type species: L. vellereus (Fr.) Fr.

L. piperatus (L. ex Fr.) S. F. Gray and related species [illegible]; *L. subvellereus* Peck; *L. deceptivus* Peck; *L. vellereus* (Fr.) Fr.

Sect. 6. **RUSSULARES** (Fr. 1821 ut sect. *Galorrhei*) Fr. 1838 (ut tribus). (*Pruinati* Quél. 1888, max. e parte). Pileus dry, or slightly viscid, often subpruinate, or slightly tomentose-subsquamulose, azonate or rarely zonate (and then mostly rufous-buff to dark cinnamon); lamellae becoming rather deep colored and consequently the spore dust distinctly visible as a paler powder on darker background; taste mild, bitter, or acrid; odor sometimes cumarinous; latex never colored from the beginning, never changing by exposure to anything but a light yellow (or else light cream from the beginning), sometimes watery or serifluous, but more often milky; margin of the pileus crenate or transparently striate, or smooth and entire; covering of the pileus not consisting of thick-walled hairs; spores strongly hete-

[illegible] *L. piperatus* in the broader sense consists of a group of species closely related to each other (at least in the southeastern states of North America) which differ constantly in minor macroscopical and certain chemical characters.

rotropic; cuticle never with Virescens-structure; latex not extremely abundant, in the contrary, often rather scarce except in very young and fresh specimens; pigment never completely absent.

Type species : L. subdulcis (Bull. ex Fr.) Gray.

Subsection Colorati Bat. (1908) (*Grisceini* Sing. 1942). Pileus tomentose squamulose and dry, not rufous-buff to deep cinnamon; taste mild to acrid; odor often sweetish, not of cumarin; pileus not transparently striate.

Type species : L. glyciosmus (Fr.) Fr.

L. griseus Peck; *L. glyciosmus* Fr. sensu Lundell & Nannfeldt (L. cyathula Fr. sensu Neuhoff); *L. Hibbardiae* (Burl.) Sacc. (L. glyciosmus Fr. sensu Neuhoff; L. confusus Lundell apud Lund. & Nannf.; *L. lilacinus* (Lasch) Fr. (with three subspecies, see *Ann. Mycol.* **40**: 125. 1942); *L. pusillus* Bres. (which is probably the same as *L. subalpinus* Kühner).

Subsection Rufini Sing. (1942). Pileus glabrous to subtomentose or thinly tomentose; latex milky, white, unchanging, acrid; pileus zonate or azonate; rufous to deep rufous cinnamon.

Type species : L. rufus (Scop. ex Fr.) Fr.

L. rufus (Scop. ex Fr.) Fr.; *L. Peckii* (Burl.) Sacc. (Lactaria, Burl.; Lactaria praezonata Murr.); *L. alachuanus* (Murr.).

Subsection Obscuratini Sing. (*Striatini* Sing. ex Heim ut *Striati*, subsectio *Pruinosorum*, typo excluso). Pileus transparently striate.

Type species : L. obscuratus (Lasch) Fr.

L. obscuratus (Lasch) Fr. sensu Neuhoff [L. obnubilus (Lasch) Fr. sensu Lund. & Nannf.], and a series of other poorly known species. The whole subsection — though well circumscribed — is in need of more special study.

Subsection Olentini Sing. (1942) (*Olentes* Bat., a subdivision of subsection *Fucati*, sect. *Pruinati*). Cheilocystidia conspicuous; pseudocystidia on the sides of the lamellae usually absent or very scarce; odor of the dried, and sometimes of the fresh carpophores strongly cumarinous; latex often watery, or serifluous, but also sometimes milky, unchanging.

Type species . L. camphoratus (Bull. ex Fr.) Fr.

L. camphoratus (Bull. ex Fr.) Fr. with var. *fragilis* Burl.; *L. serifluus* (D. C. ex Fr.); *L. rimosellus* Peck; *L. helvus* (Fr.) Fr.

Subsection Subdulcini Sing. (1942) (*Subdulces* Bat. 1908, a subdivision of subsection *Dulces* of sect. *Pruinati*). Pileus not squamulose or rimose, not subtomentose to tomentose, but always subglabrous to

subpruinate, dry, or slightly viscid, azonate, or somewhat zonate, rufous buff to deep cinnamon; pseudocystidia usually numerous on the sides and edges of the lamellae; odor not cumarinous; margin not transparently striate; latex milky to somewhat serifluous, white, or more rarely cream color, and often turning cream color or sulphureous when exposed; taste mild, bitter, or acrid.

Type species: L. subdulcis (Bull. ex Fr.) Gray.

The species belonging in this subsection represent the most difficult group within the *Lactarii*, and most of them have been interpreted and misinterpreted in various ways by different authors. The author makes no attempt to propose a specific disposal or arrangement. The reader is referred to several special papers by Romagnesi on this subject (see « Key to the Species », p. 727). Among the most important species of this group are: *L. subdulcis* auct.; *L. thejogalus* auct.; *L. aurantiacus* auct.; *L. ichoratus* auct.; *L. tabidus* auct., *L. quietus* auct., and many others.

Sect. 7. **PIPERITES** Fr. (1838 ut tribus). Pileus more or less viscid to glutinous, rarely dry and then neither velutinous nor pruinate, and not completely pigmentless; latex milky, white at first, and remaining so, or changing color (to yellow, purple, lilac, violet, olive, gray) by shorter or longer exposure to the oxygen of the air; lamellae rather pale-colored, and not strikingly powdery from the light colored spore masses in age; taste subacrid to extremely acrid; pigment rarely a deep rufous buff to deep cinnamon, and odor of dried specimens never strongly cumarinous; margin of the pileus never transparently striate; covering of the pileus not consisting of thick-walled hairs; spores strongly heterotropic; cuticle never of the Virescens structure; latex not extremely abundant but fairly abundant in adult specimens under normal growth conditions; pigment rarely completely absent.

Type species: L. torminosus (Schaeff. ex Fr.) Gray.

Subsection **Pyrogalini** Sing. (1942). Latex unchanging; pileus dull colored, often not viscid.

Type species: L. pyrogalus (Bull. ex Secr.). Fr.

L. pyrogalus (Bull. ex Secr.) Fr. and its various subspecies (see *Ann. Mycol.* 40: 123. 1942); perhaps also *L. circellatus* Fr.

Subsection **Insulsini** Sing. (1942) (« Group » *Insulsae* Burl. p. p. 1910; « Groupe » *Immutabiles* Konrad et subsection *Glabrati* Bat.).

Type species : L. insulsus (Fr.) Fr.

Note : This section is closely related to certain species of the *Russulares*, e. gr. *L. quietus* and some *Rufini*.

Stirps **Insulsus** (Pileus slightly pubescent on the extreme margin, or more frequently wholly glabrous).

L. controversus (Pers. ex Fr.) Fr.; *L. pallidus* (Pers. ex Fr.) Fr.; *L. insulsus* (Fr.) Fr.; *L. roseozonatus* (v. Post ex Fr.) Britz. (L. flexuosus var. roseozonatus v. Post ex Fr.); *L. hysginus* (Fr. ex Fr.) Fr.; *L. Porninsis* Rolland; *L. musteus* Fr.

Stirps **Torminosus** (Margin barbate).

L. torminosus (Schaeff. ex Fr.) Gray, ssp. *eutorminosus* Sing. and ssp. *pubescens* (Fr.) Konr. & Favre; also obviously *L. Mairei* Malençon.

Subsection Croceini Sing. (1942) («Group» *Croceae* Burl.). Latex changing to bright yellow after a short time of exposure.

Type species : Lactaria crocea Burl.

Stirps **Chrysorheus** (Pileus slightly pubescent or glabrous on the margin).

L. chrysorheus Fr. and its American satellites, such as *Lactaria crocea* Burl. etc. (perhaps not all of them worthy of specific distinction).

Note : This stirps is closely related to certain species of the *Russulares*, e. gr. *L. thejogalus*, and represents a continuation of the *Subdulcini* in the same manner as subsection *Insulsini* is a continuation of certain groups in the *Russulares*.

Stirps **Scrobiculatus** (Margin barbate).

L. resimus Fr.; *L. scrobiculatus* (Scop. ex Fr.) Fr.

Subsection Aspideini Sing. (1942) («Groups» *Aspideae* and *Speciosae* Burl.). Latex becoming violet, slate lilac, purple when exposed to the air, or the context staining in one of these colors when bruised.

L. aspideus (Fr. ex Fr.) Fr.; *L. aspideoides* (Burl.) Sacc. (perhaps not specifically different from the preceding species); *L. uvidus* (Fr. ex Fr.) Fr.; *L. luridus* (Pers. ex Fr.) Gray; *L. psammicola* A. H. Smith; *L. repraesentaneus* Britz.; *L. speciosus* (Burl.) Sacc. (perhaps not specifically different from the preceding species).

Subsection Vietini Sing. (1942) («Groupe» *Vieti* Konrad of subsection *Glabrati* Bat.). Latex or context turning gray, olive or sordid pale ochraceous on exposure (often only after considerable time); pileus and stipe often gray or green.

Type species : L. vietus (Fr.) Fr.

Stirps **Trivialis** (Pileus subviscid to viscid, with glabrous margin;

L. victus (Fr.) Fr.; *L. trivialis* (Fr. ex Fr.) Fr; probably also *L. akanensis* Imai; possibly also *L. umbrinus* (Pers. ex Schw.) Fr.

Stirps **Blennius** (Pileus glabrous, strongly viscid; mycorrhiza with broad leaved trees, ordinarily *Fagus*).

L. blennius (Fr.) Fr. and its forms and varieties.

Stirps **Necator** (Pileus villous at the margin, more or less viscid).

L. necator (Pers. ex Fr.) Karst. [Agaricus, Pers. ex Fr., non Bull; Lactaria, Schroeter in Cohn; Lactarius turpis (Weinm.) Fr.; Agaricus, Weinm.; L. necans S. F. Gray; L. plumbeus (Bull. ex) Quél. non Fr. 1821]; *L. atroviridis* Peck.

Sect. 8. **DAPETES** Fr. (1838). Pileus more or less viscid, often zonate, often orange or violet or blue; latex milky and opaque, sometimes not forming droplets but merely a fine moisture on bruised tissue, always colored from the beginning, orange, red, purple, violet, blue; cheilocystidia often very well differentiated.

Type species: L. deliciosus (L. ex Fr.) Gray.

L. deliciosus (L. ex Fr.) Gray; *L. chelidonius* Peck; *L. pseudodeliciosus* Burl. (ut Lactaria); *L. Curtisii* Coker; *L. sanguifluus* (Paulet ex) Fr.; *L. subpurpureus* Peck; *L. paradoxus* Burl. (ut Lactaria); *L. indigo* (Schwein.) Fr.

KEY TO THE SPECIES

There are good regional keys, e. gr. Burlingham, *Mem. Torr. Bot. Cl.* **14**: 1-109. 1908; Kauffman, in *Agaricaceae of Michigan* **1**: 86. 1918; Coker, *Journ. Elisha Mitch. Soc.* **34**: 2. 1918; Imai, *Journ. Fac. Agr. Hokkaido Imp. Univ.* **43** (2): 305. 1938; Heim, *Prodrome à une flore mycologique de Madagascar I. Les Lactario-Russulées*, p. 160-161. Paris 1937 (1938); Romagnesi, *Rev. Mycol.* **4**, supplement. 1940 (« *Les Lactaires* »[13]); Lange, *Flora Agaricina Danica* **5**: 31. 1940; Singer, *Ann. Mycol.* **40**: 111-124. 1942 (it does not key out all the species of all sections).

GENERA EXCLUDENDA

The following genera are considered as dubious to a degree that their position in the *Agaricales* cannot be considered as established, or else — and this is the majority — they are well enough known to be rejected because, in the author's opinion, they do not belong in the *Agaricales* (in the sense outlined in part V) but in some other

[13] This is perhaps the best key available. It is adaptable to the survey given

order of the *Basidiomycetes.* These genera are indicated here only if they have been considered as belonging in the *Agaricales* or a corresponding group by some mycologists in the past. In the category of genera excludenda, the author includes also such genera that are most probably abnormal forms of agarics but cannot be indicated as synonyms of any particular genus.

Agaricochaete Eichelbaum, *Verhandl. Naturwiss. Vereins Hamburg* **3** (14): 38. 1906. This genus is characterized by thick lamellae which possess long aculeate bodies (setuloid cystidia or metuloids ?). These are red at the apex in the type species, *A. Mirabilis* Eichelbaum. Another species, *A. Hericium*, has also been described by Eichelbaum. Both species were collected in East Africa in the Usambara Mts. The description is not sufficient for the interpretation of these fungi. However, Eichelbaum states that he has deposited « beautiful and typical specimens of nearly all » his species at the Biological-Agricultural Institute at Amani. There might be a chance that these specimens are still available.

Arenicola Vel., *Nov. Mycol. Noviss., Opera Bot. Cech.* **4**: 62. 1947. Characterized as having the spores « yellow as in *Naucoria* but globose angular as in *Rhodophyllus* », and based on *A. flavispora* Vel., this genus cannot be inserted without reexamination of the type which was not available at the time this account was written.

Arrhenia Fr., *Summa Veg. Scan.*, p. 312. 1849. This is a genus of uncertain position. It should, in the author's opinion, be understood with *A. Auriscalpium* Fr. as the type species. This is no. 1, and marked « Nobilissima » in the original account. According to Konrad & Maublanc, this has colored spores, and a species from tropical America, *Arrhenia peziziodea* (Speg.) Pat. ex Sing. (see *Lloydia*, **8**: 186-188 has reddish spore print. Wherever this genus is placed eventually, there is no doubt that it does not belong in the *Agaricales*. It is somewhat intermediate between the genus *Campanella* (*Leptotaceae*) and *Merulius* (*Meruliaceae*), however, a final decision should be made only when the whole complex of *Cyphella* is revised

Baumanniella Henn., *Engl. Bot. Jahrb.* **22**: 543. 1895. This genus is based on *B. togoensis* Henn. which is characterized as a brown-spored *Physalacria*. Since *Physalacria* is here considered as belonging in the *Agaricales*, it would be interesting to study the type of *Baumanniella togoensis*, if it still exists. The description alone does not allow any conclusions at all. Corner considers it identical with *Physalacria*.

Boletium Clements, *Gen. Fungi*, p. 108. 1909, see *Volvoboletus*.

Boletopsis Fayod, *Malphigia* 3. 72. 1889. This is based on *Polyporus melaleucus*, an obviously misspelled version of *Polyporus leucomelas* Pers. ex Fr. Donk, R. Maire, and Singer have recognized this genus, but it belongs in the *Phylacteriineae* where it is the only representative of a family *Boletopsidaceae* (Donk ut tribus) Bond. & Sing. The *Phylacteriineae*, just as other main groups in the *Aphyllophorales*, can be divided into groups with resupinate carpophore and smooth hymenial surface, pileate carpophore and smooth or rugose venose hymenial surface (*Thelephora*, and probably *Polyozellus*), spinose hymenophore (*Sarcodon* and allied genera), and with poroid hymenophore (*Boletopsis*). What Fayod says about the relationships with certain boletes should not be taken into consideration since there are no such boletes that are related to any *Aphyllophorales.*

Calyptella Quel., *Enchir.*, p. 216. 1886. As long as the type species of this genus has not been fixed, it is dificult to say anything about the standing and position of this genus. As the author understands it, it would contain a species whose type specimens the author has studied, *Cyphella musaecola* Berk. & Curt. This has membrana pigment, clamp connections, and a structure similar to that of *Leptotus*. Unless *Leptotus* is admitted to the *Agaricales*, this species would not be admitted either. However, it is recommended to wait for a more thorough study of the *Cyphella* complex, and proposals of lectotypes in the various genera before final disposals are attempted.

Campanella Henn., *Engl. Bot. Bot. Jahrb.* 22: 95. 1895. This is undoubtedly a good genus, often called *Laschia* by certain authors including Patouillard. It has been redescribed by Singer (*Lloydia* 8. 190 195. 1945) who does not consider it as a genus of the *Agaricales* for reasons discussed (l. c.). Several species are rather comparable to *Merulius*, others to *Arrhenia*, others to *Leptotus*, and some have cystidia similar to those of *Hohenbuehelia*, yet with a different behavior in cresyl blue mounts.

Cantharellus Adans. ex Fr., *Syst. Mycol.* 1: 316. 1821. The lectotype is *Cantharellus cibarius* Fr. Many species belong in other genera (*Craterellus*, *Geopetalum*, *Hygrophoropsis*, *Cantharellula*, *Gomphus*, *Leptotus*); additional species have been described since 1821 which are undoubtedly good species of *Cantharellus* sensu str. These are: *Cantharellus cinnabarinus* (Schwein.) Schwein.; *Cantharellus guyanensis* Mont. (type seen); *C. odoratus* (Schwein.) Sing. (Craterellus odoratus Schwein.); *C. lateritius* (Berk.) Sing. (Craterellus lateritius

Berk.; Thelephora Cantharella Schwein.; Craterellus, Fr. The last two species have practically smooth hymenial surface but are otherwise very close to *Cantharellus cibarius*. The spore print is always bright colored in *Cantharellus*, mostly yellow or pink. The basidia are long, with often more than 4 sterigmata, and stichic. This genus is the type genus of a small family, *Cantharellaceae*, consisting of *Cantharellus* and *Craterellus*, the latter containing — not the smooth — but the thin forms with more cartilaginous trama. Typical for these thinner forms is *Craterellus cornucopioides* (L. ex Fr.) Pers. Somewhat intermediate between *Cantharellus* and *Craterellus* is, according to external characters, *Cantharellus minor* Peck which is common from Virginia to Georgia, U. S. A. But more detailed anatomical investigations will certainly show its definitive place. The *Cantharellaceae* may be interpreted as containing only these two genera and being stichobasidial in all species, or else they may be understood in a wider sense including the *Gomphoideae* (genera with chiastobasidia). In either case, they are not related to the *Agaricales* but to the *Clavariineae*: *Cantharellus* and *Craterellus* to *Clavulina*, and *Gomphus* to *Clavariadelphus* Donk.

Campia O. Kuntze, *Rev. Gen. Pl.* 3: 151. 1898. The type species is *Campia Montagnei* (Berk.) O. Kuntze. This species is often indicated as *Hypolyssus Montagnei* Berk. However, Berkeley was wrong using Persoon's generic name *Hypolyssus* for his tropical American species as was correctly shown and remedied by O. Kuntze. The genus *Campia* is one of the most interesting forms of the neotropics. It is rarely found in sporulating condition, but the author was able to discover a good specimen from Panamá with fertile hymenial surface. This specimen was compared with the type and with authentic material.

The spores are smooth, ellipsoid, with suprahilar applanation, heterotropic, hyaline to stramineous hyaline, nonamyloid, 4.8-5.8 × 2.2-3, mostly about 5.3 × 2.7 µ; basidia clavate, 21 × 5.3-5.5 µ, sterigmata not seen, without septa; cystidia none; surface of the « pileus » sterile, but no cuticle differentiated, and no dermatocystidia or other specialized bodies present; tissue of the upper portion of the carpophore consisting of irregularly intermixed, thick walled hyphae which are nonamyloid. In spite of the fact that this fungus has often been compared with the agarics, or considered as close to them, the author is convinced that it belongs in the family *Stereaceae*, together with *Stereum*, *Skepperia*, and similar genera.

Cheilophlebia Opiz & Gruntl., *Lotos* 7: 107. 1867. When reading the diagnosis of this genus, one is inclined to guess that it belongs in the *Hemimyceneae* or *Myceneae* (tribus of the *Tricholomataceae*), perhaps in the group of small venose species of *Marasmiellus*. However, lacking specimens to substantiate this guess, one is at a loss to prove it, and *Cheilophlebia* remains a nomenclatorial threat as long as it is not — as it should be — rejected in favor of those well defined genera which it might possibly replace because of the early date of publication. The author proposes to put *Cheilophlebia* on the list of genera rejicienda.

Chloroneuron Murr., *Mycologia* 3: 25. 1911 is merely a new name for the following genus.

Chlorophyllum Murr., *North Am. Fl.* 9: 172. 1910, non Massee (1898). This genus is based on *C. viride* (Pat.) Murr. (*Necrophyllum viride* Pat.). Murrill's generic name is a homonym, the type species is not an agaric. See also genera *Chloroneuron*, *Gomphus*, and *Necrophyllum*.

Clavulinopsis Van Overeem, *Bull. Jard. Bot. Buitenzorg* III, 5: 278. 1923. This is a clavariaceous genus, and according to Donk synonymous with *Clavulina*, in any case very close to the latter. It must have slipped by mistake into the genera of *Agaricaceae* (Clements & Shear).

Collyria Fr., *Summa Veg. Scan.*, p. 340. 1849. According to Patouillard, this genus was probably established for a monstrosity of the type *Stylobates* (see under that genus, below). If this is correct, it would have to be rejected according to Art. 65.

Corniola S. F. Gray, *Nat. Arr. Brit. Pl.* 1: 637. 1821, non Adans. (1763). The type is *C. lobata*. This is a homonym of *Corniola* Adans. and a synonym of *Leptotus* Karst.

Cyclocybe Vel., *Nov. Myc.* p. 122. 1939. A doubtful genus, characterized as an annulate *Inocybe*.

Daedalea Pers. ex Fr., *Syst. Mycol.* 1: 331. 1821. This genus has been regarded as being close to *Agaricus* in the Linnean sense by some of the earlier authors. Later authors have referred it to the *Polyporaceae*, and in spite of various emendations and the probable transfer of the genus *Polyporus* itself to the *Agaricales*, *Daedalea* must be considered as belonging to the *Aphyllophorales*. It is close to *Daedaleopsis*, *Coriolopsis*, *Whitfordia*, and various other genera, including *Acrotus* Fr. (see there), and together with another group (*Coriolus*, *Microporus*, *Trametes*, *Pseudotrametes*, *Lenzites*, etc.), it

forms one of the main subdivisions of the polypores, the *Corioloideae*. The type species of *Daedalea* is *D. quercina* (L.) Pers. ex Fr. Some species of *Daedalea* are foreign to that genus: *D. elegans* Spreng. ex Fr. is *Whitfordia elegans* (Spreng. ex Fr.) Sing.; *Daedalea confragosa* (Bolt., Pers. ex Fr. is *Daedaleopsis confragosa* (Bolt.) Schroeter; *Daedalea unicolor* (Bull. ex) Fr. is *Cerrena unicolor* (Bull. ex) Murr.; *Daedalea philippinensis* Pat. is *Diacanthodes philippinensis* (Pat.) Sing. etc., but none of all these is a species of the *Agaricales*. However, *Daedalea meruloides* Schwein. is *Gyrodon meruloides* (Schwein.) Sing.

Dictyolus Quel., *Enchiridion*, p. 139. 1886. This is a synonym of *Leptotus* Karst. (see there).

Favolaschia Pat., Henn., *Engler's Bot. Jahrb.* 22: 93. 1895. This genus is not, as assumed by Patouillard, closely related to *Marasmius* (*Androsaceus*) and the *Mycenae*. If there is any relationship at all, it would be between *Favolaschia* and the *Panelleae*. But even this affinity is at present not actually substantiated. In the author's opinion, *Favolaschia* is closer to *Aleurodiscus* and *Campanella* and also certain *Cyphellae*, and probably *Leptotus*. This whole group has been called *Leptotaceae* in the past but this may merely be a temporary name, valid only as long as the taxonomy of the *Aphyllophorales* remains unrevised. *Favolaschia* is distinguished from *Campanella* by amyloid spores, pit-like, round pores which at maturity become favoloid; often also by the presence of dendrophyses and gloeocystidia. The type species is *F. Gaillardii* Pat. Aside from it, the following species are well known: *F. rubra* Bres. Pat.; *F. tonkinensis* Pat.) Sing.; *F. pustulosa* (Jungh.) Sing.; *F. varariotecta* Sing.; *F. Sprucci* (Berk.) Sing.; *F. saccharina* Pat.; *F. cinnabarina* (Berk. & Curt.) Pat.; *F. pezizoidea* (Berk. & Curt.) Pat. ex Sing.; *F. sabalensis* (Charles) Sing.; *F. Thwaitesii* (Berk. & Br.) Sing. (with several subspecies): *F. pygmaea* (Speg.) Sing.; *F. Puiggarii* (Speg. Sing. As for complete descriptions, keys and a history and discussion of the genus and species, see Singer, *Lloydia* 8: 170-230. 1945.

Friesula Speg., *An. Soc. Cient. Argentina* 8, 284. 1880. This genus is said to be identical with *Skepperia* (see Patouillard, *Essai*, p. 141. 1900). The type species, *F. platensis* Speg. (*l. c.*) from Argentina has been studied by the author, and was found to be generically different from *Skepperia*. Its anatomical characters suggest a position somewhat intermediate between *Cytidia* and *Skepperia*. Neither genus belongs in the *Agaricales*.

Galeromycena Vel., *Nov. Myc. Noviss., Opera Bot. Cech.* **4**: 66. 1947. «Color reminiscent of *Laccaria* but... spores similar to those of *Galera...*». Type species: *G. mirabilis* Vel. Type material not available at present.

Galeropsina Vel. *Nov. Myc. Noviss., Opera Bot. Cech.* **4**: 74. 1947, nom. nud. Some ochrosporous agaric (?).

Galeropsis Vel., & Dvorak apud Vel., *Mykologia* **7**: 106. 1930 (*Psammomyces* Lebedeva 1932). This is an interesting fungus like *Cyttarophyllum*, but more gastroid, without cheilocystidia and with a somewhat tougher consistency; the spores are attached to elongate, subflexuous straight sterigmata in the manner of the *Gastromycetes*. For more data see Singer, *Beih. Bot. Centralb.* **56** (B): 147-149. 1936. *Galeropsis desertorum* Vel. & Dvorak apud Vel. and *G. plantaginiformis* (Lebedeva) Sing. are thus far the only old world species known in this genus, and it is possible that the latter is only a form of the former. A South American species without germ pore is *G. allosperma* Sing. [Galera paradoxa Speg., non Galeropsis paradoxa (Mattiroli) Heim].

Gloeocantharellus Sing., *Lloydia* **8**: 140. 1945. The type of this genus, *G. purpurascens* from Tennessee, U. S. A., was first described as *Cantharellus*, and is consequently a former agaric. This is the reason why this genus has been inserted in the list of genera excludenda. *Gloeocantharellus* differs from *Gomphus* and *Chloroneurum* in the presence of gloeocystidia and in more lamellate veins.

Gomphus S. F. Gray, *Nat. Arr. Brit. Pl.* **1**: 638. 1821. The species of *Gomphus*, already distinguished in Persoon's time, were often confused with *Cantharellus* and *Craterellus*, from which they differ in the large spores whose wall becomes rugose after dehydration in the herbarium, or else is rugose (often reticulate-rugose) from the beginning (except for the immature spores); they also differ in the more rugose-venose-reticulate configuration of the hymenophore, chiastobasidia instead of stichobasidia, and a very fleshy, thick carpophore. The following species are typical for *Gomphus*: *G. clavatus* (Pers. ex Fr.) S. F. Gray; *G. crassipes* (Dufour) R. Maire; *G. Bonarii* (Morse) Sing.; *G. floccosus* (Schwein.) Sing. The genera closest to *Gomphus* are *Chloroneurum* Murr. and *Clavariadelphus* Donk. The former differs in more strongly ornamented spores and the presence of some cystidia (not gloeocystidia), and may also be considered as a subgenus or section of *Gomphus* (as it was done by Patouillard who distinguished under *Nevrophyllum* — a synonym of *Gomphus* — a

group (A.) without cystidia and with the spores smooth when fresh, and a group (B.) with projecting cystidia and reticulate spores. The latter group corresponds to *Chloroneurum*. The hyphae are clamped and non-amyloid in both groups; the spores are deep yellow and non amyloid; the upper surface of the carpophores is non-differentiated. All these characters can also be found in *Clavariadelphus* which differs from *Gomphus* in the club-shaped carpophores which are sometimes somewhat truncate at the apex. Because of this shape, they are usually considered as belonging to the *Clavariaceae* but they have a different spore type and never occur coralloid, or ramose.

Graminicola Vel., *Nov. Myc. Nov.*, *Opera Bot. Cech* **4**, 81. 1947. « Very slender small fungus ...spores globose, small, reddish... » Based on *G. gracilis* Vel. from Czechoslovakia.

Hemigaster Juel., *Sver. Vet. Akad. Handl* **21** 111. 1895. This is based on *Hemigaster candidus* Juel. on rabbit dung in Sweden. This fungus is somewhat controversial; the author has not seen any specimens. The fungus is small, passes through a gymnocarpous phase, and becomes then persistently angiocarpous; aside from basidiospores, « gemmae » (probably chlamydospores) are formed; a columella, and a powder, consisting of mature basidiospores and gemmae is found inside the peridium of the adult specimens. This may be a new genus intermediate between *Gastromycetes* and *Agaricales*, or else a gastroid form of some agaric comparable with the gastroid forms of *Boletinus decipiens*. In fact, Thaxter who collected this latter in Florida, called his specimens *Hemigaster* sp. Bresadola seemed to think that *Hemigaster* is merely a young stage of a *Coprinus* sp.

Hymenogramme Berk. & Mont., apud Mont., *Syll. Crypt.*, p. 151. 1856. This is based on a species of « *Poria* », or rather a resupinate representative of the *Coriolоideae* (polypores), and Saccardo & Cuboni add *Laschia crustacea* (Junghuhn). This genus as well as *Lenzites* to which it is said to be related, are *Aphyllophorales* and have nothing in common with the *Agaricales* except the configuration of the hymenophore.

Hypolyssus Pers., *Mycologia Europaea* **2**: 6. 1825. The type species is *H. ventricosus* Pers. This is a combination of an agaric with its parasite, and must therefore be considered as either a monstrosity provoked by the *Hypomyces*, or else a nomen confusum (its characters deriving from two different genera), according to Art. 64 and 65 of

the International Rules. It is impossible to remodel this genus so as to be the valid generic name for *Caripia*.

Laschia Fr., *Linnaea* 5: 533. 1830. This genus is a synonym of *Auricularia* since the type species, *Laschia delicata*, is congeneric with *Auricularia auricularis*. However, as in the case of *Hypolyssus*, later authors have disregarded the original concept, and have given the genus another sense. *Laschia* in the sense of Patouillard is *Campanella* Henn. *Laschia* in the sense of Lloyd is the sum of *Filoboletus* and *Favolaschia*. *Laschia* Junghuhn is a homonym of *Laschia* Fries. It was described four years after the latter. It contains one species which might be congeneric with *Hymenogramme*, and one which is a synonym of *Polyporus vibecinus* Fr.

Lenzites Fr., *Gen. Hymen.*, p. 10. 1836. This genus has been restricted to *L. betulina* (L. ex Fr.) Fr. and related forms. It is very close to *Coriolus* and differs in the presence of cystidia, while *Coriolus* has hyphal pegs, or no sterile elements at all. The hymenophore in *Lenzites* is more or less lamellate, but this does not mean that *Lenzites* is related to *Lentinus* and other similar *Agaricales*.

Leptoglossum Karst., *Hattsr., Bidr. Finl. Nat. Folk.* 32: xvii. 1879; non *Leptoglossa* D. C. 1841, nec *Leptoglossum* Cooke (at subgenus; 1879). This is congeneric with the following genus and with *Dictyolus* Quél. The author prefers the following genus since there might be misunderstandings as to which genus is meant if *Leptoglossum* in the sense of Karsten were accepted. If there were no choice, Karsten's *Leptoglossum* would have to be accepted since it is perfectly legal. But as there is a choice between two generic names published in the same paper, *Leptoglossum* is here rejected.

Leptotus Karst. *l. c.* This genus is closely related to *Campanella* from which it differs in its bryogenous habit and less anastomosing lamellae or veins. Some of the species belonging here have been mistaken for *Omphalina* (*Omphalia muralis* sensu Ricken for which the new name *Leptotus Rickenii* Sing. is proposed) and for *Pleurotus*, e. gr. *Leptotus tremulus* (Schaeff. ex Fr.) Sing. (Pleurotus, Quél.), but some others, with less conspicuous carpophores and hymenophores, have been called *Cyphella*. The genus *Leptotus* is scarcely a true representative of the *Agaricales*. The author is not prepared to tell whether it has affinities in the *Corticiaceae*, or *Meruliaceae*, or some of the groups which will eventually result from the dismemberment of the *Cyphellaceae*; it is somewhat related with *Campanella*, and this latter is somewhat related with *Favolaschia*. These genera have

been combined on a temporary basis in the family *Leptotaceae* R. Maire em. (see Singer, *Lloydia* **8**: 170-230. 1945, especially p. 189). The trama of the species of *Leptotus* is rather intermixed-interwoven, consisting of only one kind of non-gelatinized (fundamental) hyphae; the pigment, where present, is a membrana-pigment which is not easily dissolved; clamp connections are either present or absent, according to the species. The sterigmata are rather long, and the basidia are devoid of carminophilous granulosity; the spores are of various shapes and sizes, always smooth and nonamyloid; cystidia are not present; the cortical layer is scarcely differentiated. A stipe is sometimes present, and at times subcentral, mostly short and not well differentiated, eccentric to lateral, or in many species, absent; the hymenophore is either venose (or almost smooth) or lamellose and then strongly anastomosing or repeatedly forked. This latter character and the structure of the trama distinguish *Leptotus* from *Omphalina*.

Mapea Pat., *Boll. Soc. Mycol. Fr.* **22**: 46. 1906. The author has studied the type, *M. radiata* Pat., which is, as has been said before by R. Maire, an atypical rust fungus. The spores are typical rust spores. F. Hoehnel who once identified *Mapea* with *Marasmius corbariensis* Roumeguere was forced to repudiate this statement later.

Montagnea Fr., *Gen. Hym.*, p. 7. 1836. Many authors consider this genus as belonging to the *Agaricales*, somewhere near *Coprinus*. There is no doubt in the author's mind but that *Montagnea* is, indirectly, related with the *Coprinaceae*. However, if there is such a thing as a Gastromycete, i. e. unless we proceed dividing all the *Gastromycetes* among other groups, *Montagnea* is one of them. With the same right, we might consider *Secotium*, *Galeropsis*, *Hydnangium*, *Rhizopogon*, etc. as *Agaricales*.

Montagnites Fr., *Epicrisis*, p. 240. 1838. This is a synonym of *Montagnea*. As for the nomenclatorial aspect of the *Montagnites*-problem, see Montagne, *Syll. Crypt.*, p. 130. 1856.

Mycenopsis Vel., *Nov. Myc. Nov.*, *Opera Bot. Cech.* **4**: 35. 1947. No generic description is given, but the only species, *Mycenopsis globispora* Vel. from Czechoslovakia, is described. The description is insufficient according to modern standards in the *Mycena* group (to which this fungus is supposed to belong), and type material is at present not available.

Mycobonia Pat., see under *Pleurotus* (p. 269) and *Porodisculus* (p. 283-284).

Necrophyllum Pat., *Hym. Eur.*, p. 129. 1887. This is a synonym of *Gomphus* (see there).

Perona Pers., *Mycologia Europaea* **2**: 3. 1825. Albertini & Schweinitz wrote in a note (p. 351. 1805) that one of their sections of *Helotium* is not typical for that genus and should perhaps better be taken into a separate genus. This is what Persoon did in 1825. He added two species described by Tode, also as *Helotium*. This genus consists of what appears to be exceptional agarics with smooth hymenial surface. As such, they may be abnormally developed or retarded fructifications of various species and genera, but when reading carefully the descriptions and investigating the somewhat inept figures, one is inclined to think that it is an assembly of species of *Marasmiellus* (*M. ramealis*, and white species like *M. crispulus*), *Marasmius* (like *M. epiphyllus*, as suggested by Albertini & Schweinitz themselves), and *Delicatula*. Since the possibility of abnormal forms cannot be disproved, and even the determination of these fungi as *Basidiomycetes* is due more to the general appearance and consistency of these carpophores such as they were described than to any type studies, it would not seem right to risk the chance of this genus replacing one of the established or well defined genera of the *Agaricales*. The genus *Perona* is perhaps a later homonym and probably a « nomen dubium » and does not endanger any agaric genera. But *Helotium*, as it is, unprotected by conservation, would possibly become another generic name competing for the legal name of *Marasmiellus*.

Phaeohygrocybe Henn., *Engler's Bot. Jahrb.* **30**: 50. 1901. Hennings's diagnoses are so incomplete and so unreliable, it is impossible to tell whether this is a valid genus of the *Agaricales* as Hennings believed it to be. When reading the diagnosis one is tempted to think that *Phaeohygrocybe* might be the same as *Neopaxillus*. But without specimens no such conclusion can be substantiated. It is not even certain that this is an agaric.

Phlebophora Lév., *Ann. Sc. Nat.* II. **16**: 238. 1841. Hymenophore venose. This is an anomaly common in agarics, and, according to Patouillard, it is the cantharelloid deformation of the white-spored agarics while *Ptychella* is that of the brown spored agarics. The type species was found near Paris and named *P. campanulata* Lév. Quelet says that this is the deformation of *Tricholoma resplendens*. If this is so, the conservation of *Tricholoma* becomes even more important since it is not quite certain whether the venose forms in the agarics are actually monstrosities in the sense of Art. 65 of the International

Rules. If *Tricholoma* is not conserved, *Phlebophora* may replace it.

Pleurotopsis (Henn.) Earle, *Bull. N. Y. Bot. Gard.* 5 : 412. 1909. The type, *Marasmius spodoleucus* Berk. & Br. (Plicatura, Sing.) is congeneric with *Plicatura crispa* (Trogia crispa of many authors), and must be considered as belonging in *Plicatura* unless it is shown that *Plicatura Alni* is not congeneric with *Plicatura crispa*. If so, both *Plicatura crispa* and *P. spodoleuca* would enter the genus *Pleurotopsis (Meruliaceae)*.

Polyozellus Murr., *N. Am. Fl.* 9 : 171. 1910. The type species, *P. multiplex* (Underwood) Murr. has been studied by the author but unfortunately some material was chosen that seems to be misdetermined. The majority of the material has small spores of the kind found in *Thelephora* and *Calodon*. Though the fungus is strongly reminiscent of *Gomphus* macroscopically (hence the misdeterminations), it is quite possible that a transfer to the *Thelephoraceae* is necessary.

Polyporoletus Snell, *Mycol.* 28 : 467. 1936; cf. *Mycol.* 37 : 124. 1945.

Porolaschia Pat., *Essai*, p. 138. 1900. The type of this genus is congeneric with *Favolaschia* according to Singer (1945).

Pseudofavolus Pat., see under *Pleurotus* (p. 269) and *Porodisculus* (p. 283-284).

Pseudohygrophorus Vel., *Nov. Myc.* p. 28. 1939. Based on *P. vesicarius* Vel. from Czechoslovakia. Doubtful.

Pterophyllus Lév., *Ann. Sc. Nat.*, III. 2 : 178. 1844. *P. Bovei* Lév., the type, is said to be an anomaly of *Pleurotus ficicola* (Mont.) Sacc. (according to Patouillard). This anomaly consists in the production of lamellulae on the two sides of the normal lamellae.

Ptychella Roze & Boudier, *Bull. Soc. Bot. Fr.* 26 : lxxiv. 1879. This is based on *Ptychella ochracea* Roze & Boudier, a fungus which, according to its authors, « has the external habit, appearance and color of » *Agrocybe pediades*, especially when young but the lamellae are those of *Cantharellus*, *Nyctalis*, etc. This is, also according to Patouillard, a not uncommon monstrosity of brown spored and black-spored agarics; in this particular case, it is probably a phlebophoroid aberration of *Agrocybe vervacti*, a species not uncommon in France.

Raddetes Karst., *Hedwigia* 26 : 112. 1897. « a gelatinous, stipitate fungus; hymenophore continuous with the stipe, descendent into a minutely cellular trama; stipe central; lamellae simple, attingent; partial veil floccose-glutinous, thin. » Karsten. This genus is based on *R. turkestanicus* Karst. from Ashkhabad, Middle Asia. The pileus

is said to be subcampanulate cylindric; spores were not seen. Lebedeva compares her *Psammomyces* (i. e. *Galeropsis*) with *Raddetes* but the spores are too obvious in any secotiaceous fungus to be overlooked. Saccardo identifies it with *Stylobates* which is not a great help since *Stylobates* is just as puzzling as *Raddetes*. If there is a type in Finland, the question might still be solved

Rhacophyllus Berk., *Journ. Linn. Soc., Botany* 11: 559. 1871. This has thin small carpophores with a finger shaped pileate portion and a stem which is thin but dilated at the base. The pileate part is cartilaginous, striate or even split, bright lilac colored, and instead of any kind of hymenophore, it merely consists of minute loculi and lobes, there is no trace of basidia or spores; yet the fungus is evidently mature. These sclerotized lens shaped cells are very thick walled, and arranged in the manner of lamellae, yet the interlamellar spaces and most of the trama are also transformed into sclerotized cells. The specimens preserved in the Patouillard Herbarium do not belong to the type species of *Rhacophyllus*, i. e. *R. lilacinus* Berk., but to another species of the same genus. These specimens are inserted under « *Psathyra* [*Psathyrella*] *gyroflexa*, bulbillosis ».

There are no specimens of « bulbillosis » under *Psathyrella disseminata* in Patouillard's Herbarium at the Farlow Herbarium. No specimens are preserved that show the derivation of the non sporulating form from a normal form. However, the author is rather skeptical on the question as to whether *Rhacophyllus* is a valid name and thinks it should be regarded as a stage or condition belonging to some *Agaricales*. It is quite true that the carpophores are agaric-like in habit and appearance but this in itself is not a valid reason to consider them agarics. Moreau (1913) studied the cytology of Patouillard's specimens, and it appears that reduction division is taking place in the bulbils which are at first binucleate. The one nucleus resulting from fusion of these nuclei divides twice, but two of the nuclei degenerate and the final stage is binucleate just as the initial one. Moreau concludes that Patouillard is right regarding these bulbils as organs of propagation. This is evidently so, since the cytology of the bulbils seems to be very much in the pattern of that of the basidium. The second, and even more forceful reason why the cases of bulbilosis are nothing but an abnormal stage of certain agarics, is the following: While at the locality where the author collected *R. lilacinus* (Kelley's Hammock, Alachua Co., Florida), no other species were observed which were even remotely comparable

with the *Rhacophyllus*, the author collected an interesting new species of *Marasmius*, *M. spinosissimus* Sing. in the subtropical montane forest of the Selva Boliviano Tucumana in Argentina in which the very young stages showed normal development of basidia and basidiospores while in a somewhat later stage of the same specimen the transformation of the apical subhymenial cell into bulbils began and no more spores were formed. The carpophores became «*Rhacophyllus* forms» and lost their fragile membranous consistence. In a very old specimen, the author observed germination of the bulbils. In the light of these observations, the hypothesis suggested by Moreau and Patouillard, and accepted by Gaumann and others, can now be regarded as proved to be correct, and one cannot help but remember a rather similar phenomenon discovered by Heim (1932) in *Podaxon* where the basidia are transformed into pseudobasidia (i. e. basidia which are hypertrophic, sclerotized, and evidently taking over something of the aspect and rôle of the basidiospores).

Rimbachia Pat., *Bull. Soc. Myc. Fr.* 7: 159. 1891. The type species, *R. paradoxa* Pat. from Ecuador, has been described by Patouillard (l. c. and *Essai taxonomique*, p. 131. 1900), and Singer (*Lloydia* 8: 186. 1945); both accounts are based on the type material. This genus is cupuliform and stipitate; the hymenial surface is nearly smooth or slightly veined; the trama and spores are nonamyloid, the latter smooth, hyaline and ellipsoid, the hyphae with clamp connections, the outside of the cup sterile, and the walls of the hyphae not strongly thickened. Patouillard has inserted this species in the *Cantharellés*, but it must be kept in mind that his *Cantharellés* are a very heterogeneous unit containing *Cantharellaceae* as well as *Leptotaceae* and true *Agaricales*. Whether or not *Rimbachia* is recognized as an agaric depends on the final disposal made of the genus *Leptotus* itself. As long as *Leptotus* is kept out of the *Agaricales*, *Rimbachia* and allied genera such as *Arrhenia* (sensu Sing. *Lloydia*, l. c.), *Campanella* and some *Cyphellae* must be kept out of that order also. Pilát (1927) erected a genus for *Craterellus spathularius* Berk. & Curt. which he called *Skepperiella spathularia* (Berk. & Curt.) Pilát. The author has studied the portion of the type preserved at the Farlow Herbarium (Curtis Herbarium), and also better material collected by Thaxter on Trinidad (on *Nostoc*, covering rocks). Microtome sections show that the inside of the spatulate portion of the carpophore is fertile and the outside is sterile. The structure of the outside is not quite as described by Patouillard but consists of interwoven to sub

parallel hyphae which may, at places, emit a few hair-like excrescences or be irregularly and minutely rough but this is not reason enough to compare this species with *Skepperia* (as a species of which it was considered by Patouillard) or *Marasmius*. In the contrary, the whole structure, reactions, and appearance of these fungi is so much like *Rimbachia* that the author has not the slightest doubt but that they are congeneric with the latter. *Rimbachia spathularia* (Berk. & Curt.) Sing differs from *R. paradoxa* in smaller spores (6-7 × 4-4.2 µ, rarely somewhat larger or smaller). The subhymenium is a broad layer of very irregular, very strongly and intricately interwoven elements which may appear to be cellular when observed hastily. Between this layer and the surface of the sterile (convex) outside of the cup, there is a layer consisting of much less interwoven, in fact almost parallel, rather thin walled hyphae with numerous clamp connections. The hyphae of this layer, the trama proper, are much looser organized than the remaining parts of the carpophore, yet they are not gelatinized. *Rimbachia* differs from *Arrhenia* in the sense of Singer by the absence of thick walled elements, by the much smaller size, the almost smooth hymenial surface and the straight (not nutant) stipe; furthermore, the spores are red or yellow in print in *Arrhenia pezizoides* and the other tropical Arrhenias, and they are also said to be colored in the European species (*A. auriscalpium*, according to Konrad & Maublanc). *Rimbachia paradoxa* and *R. spathularia* are both white in all parts when fresh or revived, somewhat cream-alutaceous when dried. As in *Arrhenia*, there is in *Rimbachia* a certain degree of variability as far as the shape of the carpophore is concerned. We may, for the sake of comparison, liken *Rimbachia* to *Peziza*, and *Skepperiella* to *Otidea*. Both *Skepperiella* and *Otidea* are weak genera at least in regard to the main distinguishing feature, the spatulate instead of pezizoid habit. It is the author's conviction that the degree of asymmetry in the cups of both the *Basidiomycetes* and the *Ascomycetes* is not so much a constant, genotypic character as rather an individual character depending on such factors as the position of the surface of the substratum, etc. Pilát (*l. c.*) also described a supposedly non tropical species of *Skepperia* proper, *S. carpatica* Pilát for which he proposed a special section *Hypocystidiatae* Pilát. The author has not seen the material but he is inclined to believe that *S. carpatica* is — though definitely related to *Skepperia*, as both *Skepperia convoluta* and *S. carpatica* are *Stereaceae* — neither congeneric with *Skepperia* nor with *Skepperiella Rimbachia*, but per-

Secotium G. Kunze, *Flora* 23: 321. 1840. This well known genus of the *Gastromycetes* is based on *Secotium Gueinzii* G. Kunze from South Africa. This, according to Corda, has smooth, thick walled, very pale (yellowish hyaline), short spores without germ pore. When the genus *Secotium* is revised in a critical manner, it is likely to be divided into several autonomous genera. The author is personally acquainted with *Secotium agaricoides* (Czern.) Hollos, *S. magellanicum* Thaxter *ined.* [99], *S. nubigenum* Harkness [100], and *S. tenuipes* Setchell, the latter differing from all other species in having a saccate perisporium which, together with the deep rusty (exosporial ?) ornamentation, imbedded in the perisporium, separates from the episporium under pressure. The gleba is exposed below in a fairly early stage but a cortina-like veil is noticeable in young carpophores. These *Secotia* are more or less agaricoid in appearance and anatomy, and a further appreciation of their affinities will be possible only after a revision of *Secotium*. It must be kept in mind that the generic name *Secotium* must be reserved for the group containing *S. Gueinzii*.

Skepperia Berk., *Trans. Linn. Soc., London* 22: 130. 1859. If the type species is *S. convoluta* — and it is impossible to consider any other species as such —, *Skepperia* cannot be considered as a genus of the *Agaricales* as has been suggested by Patouillard. The palisadic layer on the outside of the convolute mitruloid carpophore consists of inflated, round bodies with a deeper colored inner, and a colorless outer layer of the wall in the upper portion; the hyphae are non-amyloid and with clamp connections; the basidia are rather long, with the lower portion often decurved; spores were not found in the type specimen at the Farlow Herbarium. It shall not be denied that perhaps some other species described in *Skepperia* have closer relations with the *Agaricales*, but it is the author's conviction that *Skepperia convoluta*, and thus the genus *Skepperia*, is a stereaceous fungus, i. e. it belongs in the family *Stereaceae*, together with *Stereum*, *Cyphia*, *Cladoderris*, etc. The *Stereaceae* are to the *Coriolus-Daedalea*-

[99] This species looks like a hymenogastraceous stipitate species, in age extremely like an agaric but with the gleba not strictly lamellate. The spores are warty. It has been redescribed as *Thaxterogaster magellanicum* Sing., a species related to *Cortinarius*.

[100] This species is extremely interesting. It has the usual habit of *Secotium* but the spores are distinctly different; they are smooth, small, and provided with a germ pore; the walls are rusty colored, and a paler endosporium is discernible. This species as well as *S. magellanicum* has clamp connections.

group of the *Polyporineae* what the *Thelephoraceae* are to the *Boletopsidaceae*, i. e. differing only in smooth hymenial surface.

Skepperiella Pilát, *Bull. Soc. Myc. Fr.* 43: 56. 1927 is a synonym of *Rimbachia*.

Stylobates Fr., *Afzel. Fung. Guian.*, p. 5, 1837. The diagnosis of this genus is bewildering, and if *S. paradoxus* Fr. is recognized as type species, it is impossible to tell what Fries had in his hands when describing this fungus. It may just as well have been an aberrant form of some agaric, as Patouillard thinks, as it may have been a representative of some other order. Perhaps there is some material available for further study. Meanwhile, the best one can do is accept, on a temporary basis, Patouillard's statement (*Essai*, p. 177): « Anomaly of agarics where the lamellae are continued on the upper surface of the pileus where they anastomose more or less instead of being limited to the lower surface of the pileus ». *S. paradoxus* was collected in Africa.

Tilotus Kalchbr., *Grevillea* 9: 137. 1881. This genus is not yet validly described unless one accepts Saccardo's (*Syll.* 5: 652. 1887) account as validation of the generic name. The latter is based on *T. lenzitiformis* Kalchbr. from Port Natal, Africa, and seems to be a slight deformation of *Lenzites* or *Xerotus* where the edges of the lamellae are abundantly villous. The genus is mentioned here because Saccardo treated it as a representative of the *Agaricales*.

Trigonipes Velen., *Nov. Myc.*, p. 77. 1939. Doubtful genus, based on *T. fascicularis* Velen. from Czechoslovakia.

Urceolus Velen., *Nov. Myc.*, p. 44. 1939. Doubtful genus, based on *U. sambucinus* Velen. from Czechoslovakia.

Valentinia Velen., *Nov. Myc.*, p. 38. 1939. Doubtful genus, based on *Cantharellus Valentini* Velen. from Czechoslovakia.

Vanromburghia Holtermann, *Myk. Unters. Trop.*, p. 104. 1898. Doubtful genus, based on *V. silvestris* Holtermann, a species of gelatinous consistence and with smooth hymenophore. It may be one of the reduced agarics of the *Marasmiellus*-series, but then it may belong to a different order. It is indicated here for two reasons. Saccardo put it in synonymy with *Phlebophora Solmsii*, also from Java, and *Phlebophora* is here treated as an irregularity of the carpophore formation of an agaric. Besides, *Vanromburghia* was indicated by Lloyd as a possible synonym of *Laschia caespitosa*, a species treated here as synonym of *Filoboletus manipularis*, an agaric. Both

erroneous. Lloyd himself indicated subsequently that his suggestion was based on an error. It is not known to the author if and where type material of *Vanromburghia* exists.

Volvoboletus Henn. in Engler & Prantl, *Nat. Pfl. fam.* I. 1 ** : 196. 1898. This genus is based on *Boletus volvatus* Pers. = *Volvoboletus volvatus* (Pers.) Henn. which is some species of the *Amanitaceae*, probably *Amanita* where the lamellae have been transformed into pores by a disease or an abnormality of the hymenophoral structure as it can be observed frequently in *Amanita gemmata* in Europe. *Bolitium* Clements is based on the same type.

Xerotus Fr., *Elenchus Fung.*, p. 48. 1828 (*Xerotinus* Reichenb., *Conspectus Regni Veg.*, p. 14. 1828). The type species is *X. afer* Fr. This is preserved at Uppsala from where the author received a fragment and a photograph of the type specimen. The fragment has all anatomical and chemical characters of *Gloeophyllum*. The latter genus will therefore become a synonym of *Xerotus*, and its species should be transferred to *Xerotus*. *Xerotus* contains stipitate as well as astipitate species, and the type species (from Africa) happens to be stipitate. But it has not the slightest affinity to those species (of *Anthracophyllum*, etc.) which were later erroneously dumped in the genus *Xerotus*. The true *Xeroti* are close to *Daedaleopsis*, *Daedalea*, *Coriolopsis*, etc. — all true polypores.

Zephirea Vel., *Nov. Myc. Nov.*, *Opera Bot. Cech.* 4 : 61. 1947. « Very slender, vitreous transparent, non-hygrophanous, evelate, trembling; stipe very long, capillar, smooth, ...Lam. distant, narrow, free. Spores intensely yellow, with the shape of a trapezoid, smooth. Cystidia needle shaped. » Velenovsky. The type species is *Z. fusispora* Vel. from Czechoslovakia. Type material is not available at the present time. The description alone is insufficient for its disposal.

SUPPLEMENT

During the long period of printing and editing of this manuscript (1947-1951) a very intense work of exploration has been carried out by the author in South America, and by others in North America and Europe as well as in Africa and New Zealand. It is significant that only two completely described new genera and one genus incompletely known can be added to the present work.

Genus 22 *a* **GERRONEMA** Sing.

Mycologia (in print)

Type species : Gerronema melanomphax Sing.

Characters : Habit omphaloid to clitocyboid ; pileus at least partly strongly pigmented with an intracellular dissolved pigment ; hyphae somewhat thick walled and either with or without clamp connections ; spores hyaline, smooth, non-amyloid ; lamellae decurrent, narrow ; stipe central or slightly eccentric ; spore print pure white ; hymenophoral trama persistently strongly irregular ; cystidia none ; veil none ; cuticle little differentiated with repent hyphae, forming a cutis ; context white and unchanging. On decayed wood.

Development of the carpophores : Unknown.

Area : Subtropical South America.

Limits : This genus differs from *Pleurocybella* in having elongate spores, pigmented pileus surface, and sometimes pigmented stipe, a central to subeccentric long stipe, and frequently clampless septa, strongly decurrent lamellae and a very different geographic distribution. It differs from *Armillariella* in having somewhat thick walled hyphae, more elastic toughish consistency, and combining lignicolous habitat with absence of veil and rhizomorphs. It differs from *Omphalina* (with which it has the instability of the clamp connections in common) in having constantly intracellular pigment, narrow lamellae, more toughish elastic consistency, and in contrast with the indications given by Romagnesi for the species of *Omphalina*, no external granulosity in methylene blue mounts. The genus is undoubtedly most closely related to *Armillariella* but its species are analogous to *Pleurocybella* and *Nothopanus* rather than to *Clitocybe.*

State of knowledge : The three species known at present, are completely studied in every regard except their individual development and their cytology.

Practical importance : Unknown, if any.

SPECIES

G. elasticum Sing.; *G. depauperatum* Sing.; *G. melanomphax* Sing.

KEY TO THE SPECIES

A. Clamp connections present. *G. elasticum*
A. Clamp connections absent.
B. Center deeply umbilicate; margin concolorous *G. depauperatum*
B. Center prominently papillate; margin white. *G. melanomphax*

Genus 27 a PORPOLOMA Sing.

Sydowia (in print).

Type species: *Porpoloma sejunctum* Sing.

Characters: Habit tricholomatoid; pileus dry, innately fibrillose, or with a superficial fibrillosity or granular fibrillose, or with squamules and tomentum; membrana-pigment often present, often incrusting the walls of the cuticular hyphae; clamp connections in the hyphae of the context present; lamellae sinuate to emarginate as in *Tricholoma*, rather broad to broad; spore print pure white; hymenophoral trama regular; subhymenium almost interlaced, consisting of subisodiametric and filamentous elements; stipe never eccentric, fleshy; cheilocystidia in the typical antartic species present, making the edge of the lamellae heteromorphous. On forest humus and earth under *Nothofagus*, possibly also under conifers.

Development of the carpophores: Unknown.

Area: Tierra del Fuego, probably all over the *Nothofagus* area; possibly also in the northern hemisphere (see chapter on «limits»).

Limits. This genus is most closely related with *Cantharellula*. It differs from that genus in sinuate to emarginate lamellae and from the clamp bearing subgenera of *Cantharellula* in regular tramal hyphae which are parallel with each other or almost so; it differs from the only subgenus of *Cantharellula* where species with cheilocystidia are found because the hymenophoral trama is not irregular, the lamellae not decurrent and the mycelium not lignicolous. It seems that all species of *Porpoloma* are mycorrhizal with forest trees while those of *Cantharellula* are not. Furthermore, there is a tendency of the surface of the pilei in all Porpolomas to be or become yellow, or else the surface is not glabrous. The difference between *Porpoloma* and *Cantharellula* would be even more marked, and the hiatus between the two genera more obvious if it were not for one or two northern spe-

cies which appear to be intermediate although they tend more toward *Porpoloma.* These species are *Tricholoma umbrosum* Smith & Walters and *Tricholoma elytroides* (Fr.) Karst. sensu Romagnesi. Romagnesi thinks they might be specifically identical. They are most certainly very closely related, if at all different. The important difference between them on one hand and *Porpoloma* on the other hand is the abscence of cheilocystidia in *T. umbrosum* and *T. elytroides.* The structure of the hymenophoral trama is described as subparallel to interwoven. This may be understood as the structure of old specimens, or a variable degree of interweaving. As for the mycorrhizal condition of the mycelium, there are no data available, not even field observations since these species appear to be extremely rare. The author was at first inclined to consider these species as belonging in a special subgenus of *Cantharellula.* However, the existence of a tricholomatoid genus closely related to *Cantharellula* in Tierra del Fuego throws a new light on this situation. Having seen no more than a single dried specimen of the American species, the author prefers to refrain from a transfer of either *T. umbrosum* or *T. elytroides* under the present circumstances inasmuch as it is not quite clear whether Romagnesi is correct in identifying his collection with the species described and illustrated by Fries, and whether or not *T. umbrosum* and *T. elytroides* sensu Romagnesi are synonyms. If they were to enter *Porpoloma,* it is obvious that they would have to enter another section of the genus characterized by the absence of cheilocystidia.

Another genus, not yet fully circumscribed, but evidently likewise related, is *Dermoloma* (Lange), if at all accepted. The species with amyloid spores differs in having an epithelium on the pileus, yet Josserand has observed exceptional individuals without spherocysts on the pileus. There seem to be two forms or species with nonamyloid spores, one with and the other without clamp connections. The latter is the only one the author has studied himself (see R. Singer, *Type Studies on Agarics, Lloydia* 5: 117. 1942). If it is assumed — as seems to be the tendency of the European authors — that these three species or forms are generically identical, they would perhaps enter the subgenus or genus *Dermoloma,* and by way of the amyloid form without epithelium, they would touch the circumscription of *Porpoloma*, in case *T. umbrosum* and *T. elytroides* were included in the latter. Nevertheless, it can hardly be assumed that these three species are congeneric with the Porpolomas. They differ in general appearance, in habitat (as they are certainly not mycorrhizal, being

field and meadow species), and in the structure of the epicutis. The one exceptional form mentioned by Josserand should at present not be taken too serious. It has been observed frequently that an epithelium of a hymeniform type is easily washed off by rains (as in *Agrocybe*), or its development impeded by mechanical obstacles. The genus *Dermoloma* would then, if accepted, be distinguished from *Cantharellula* by its habit and the structure of its epicutis, and the same morphological characters as well as its non-mycorrhizal character would separate it from *Porpoloma*.

The resemblance of the three species admitted here in *Porpoloma* with certain species of *Tricholoma* is such as to deceive even experienced mycologists. This striking similarity, however, is without any doubt mere convergence since there is not the slightest indication of transitional forms and several correlated anatomical and microchemical characters underscore the difference. Nevertheless, this interesting parallelism has been expressed in the specific names chosen for the species of *Porpoloma*.

State of knowledge. The three species admitted now are perfectly well known except for their individual development and their cytology.

Practical importance. Unknown, if any. Potentially important for the forester since all three species appear to be mycorrhizal with *Nothofagus*.

SPECIES

P. sejunctum Sing.; *P. portentosum* Sing.; *P. terreum* Sing.

KEY TO THE SPECIES

A. Pileus, lamellae and stipe yellow from the beginning; appearance much like that of *Tricholoma sejunctum*. ... *P. sejunctum*

A. Pileus, lamellae and stipe sometimes becoming yellow in age, but not so from the beginning

  B. Pileus innately fibrillose or rarely squamulose in the center; appearance much like that of *Tricholoma portentosum* ... *P. portentosum*

  B. Pileus distinctly squamulose over large areas; appearance much like that of Tricholomas of the *Terreum* group. ... *P. terreum*

This genus should be inserted after *Cantharellula*. The key of the genera of *Leucopaxilleae* should be modified as follows: In the line where *Cantharellula* keys out, it should say:

1. Lamellae decurrent to adnate; habit not tricholomatoid. ... *Cantharellula*
2. Lamellae emarginate to sinuate; habit tricholomatoid ... *Porpoloma*

Cuphocybe Heim, *C. R. d. seances Acad. Sciences* **230** : 2246. 1950. nom. subnud. (sine diagn. lat.): with bulbous stipe, with general veil which is adnate and persistent, appearing as appressed fibers and scales on the pileus, elongation of the stipe rapid, partial veil absent, margin of pileus striate, context light (in weight), lamellae long and abruptly decurrent by a tooth, spores argillaceous, elongated, irregular, with triple wall and tuberculous. The type species is *C. olivacea* Heim which was collected in New Zealand. It has spores 11.5-15.6 × 6.2-8.6 μ, ochraceous under the microscope, ellipsoid-amygdaliform-oblong, with a straw-colored endosporium, with a thicker ocher-brown « mesospore » (apparently our episporium, which is finely rugose (bosselé), and a hyaline episporium which expresses the tuberculose « hernies » of the lower layer on the external surface. All these data are given according to Heim's account. A similar spore was found by the author in an Argentine species, collected abundantly by Spegazzini many years ago in the Parque of La Plata (province of Buenos Aires) and described as *Inocybe platensis* Speg. This fungus has decurrent lamellae and an episporial ornamentation (i. e the persistent but easily removable hyaline outer layer of the spore wall shows verrucose elevations and crevasses) and the shape of the spores is likewise more or less amygdaliform. The exosporium forms a curious button-like formation at the apex of the spores. The fungus reminds one somewhat of a thinner, more elongate *Paxillus* or *Neopaxillus*, yet the youngest available carpophores show regular hymenophoral trama. Heim inserts his species between *Cortinarius* and *Inocybe*. We have not enough data in order to make an attempt at classification. Besides, there is no certainty yet as to the generic identity of *Cuphocybe olivacea* and *Inocybe platensis*.

The paragraph on *Cuphocybe* should be inserted after *Hebeloma* (p. 579).

Thaxterogaster Sing., *Mycologia* (in print). This is a secotiaceous fungus which has no bearing on the classification of the *Agaricales*, but the publication concerned should be consulted in connection with questions of phylogeny discussed in the Introduction. *Thaxterogaster* is closely related to *Cortinarius*, and there are numerous data suggesting that the *Cortinariaceae*, at least the *Cortinarieae* may be derived from *Thaxterogaster*.

SUPPLEMENTARY NOTE: NOMENCLATURE CHANGES VOTED AT STOCKHOM 1950

After completion of the page proof, some changes of the nomenclature rules were voted by the VIIth International Botanical Congress at Stockholm. Since the publication of the present work antedates the publication of the revised rules, the old rules are technically still valid at this moment (September 1950). Nevertheless, the attention of the reader is drawn to the following items.

1. All specific epithets should be decapitalized (proposal Van Dijk, Rec. 43).

2. « The subgenus containing the type species of a generic name must bear that name unaltered » (new Art. 26 bis). This means that e. gr. the subgenus *Eu Tricholoma* Lange em. Singer will have to be renamed *Tricholoma*. It is a bad rule because the Congress has taken it upon itself to act on this proposal before the question of the lecto-type list was settled, and because it is in contradiction with Art. 3 and 4 (1). But since it has been accepted, we shall probably have to bear the consequences.

3. « If a taxon of whatever lower rank than the species which includes the type of the species is to be referred to by name, it must be designated by the correct specific epithet of the species but contrary to Art. 26 without citation of an author's name. » This rule is likewise in contradiction with Art. 3 and 4 (1) since any slight change of opinion regarding the characters of the type, or introduction of more precise information on it will cause name changes in the infraspecific ranks. According to the new article, *Russula emetica* ssp. *euemetica* Sing. will be called ssp. *emetica*.

4. The word « apud » formerly used in author citations according to Art. 48 is now replaced by the word « in » in all cases.

5. More important changes regarding the starting point of mycological literature, nomenclature of imperfect forms, etc., voted by the Special Committee on Mycology, will have little effect on the text of this book.

6. The question of validity of pre-starting point types has been solved in the sense advocated in the introduction of this work.

7. The question of the lecto-types of Gill Fungi and the « Nomina Generica Conservanda » has not been completely worked out by the Congress itself. There was, however, a favorable vote in regard of the preservation of *Marasmius* Fr., *Panus* Fr., *Pleurotus* (Fr.) Quél., and no negative vote concerning our proposals.

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[169] Starred works can be used for the acquisition of a more elementary knowledge of the subject.

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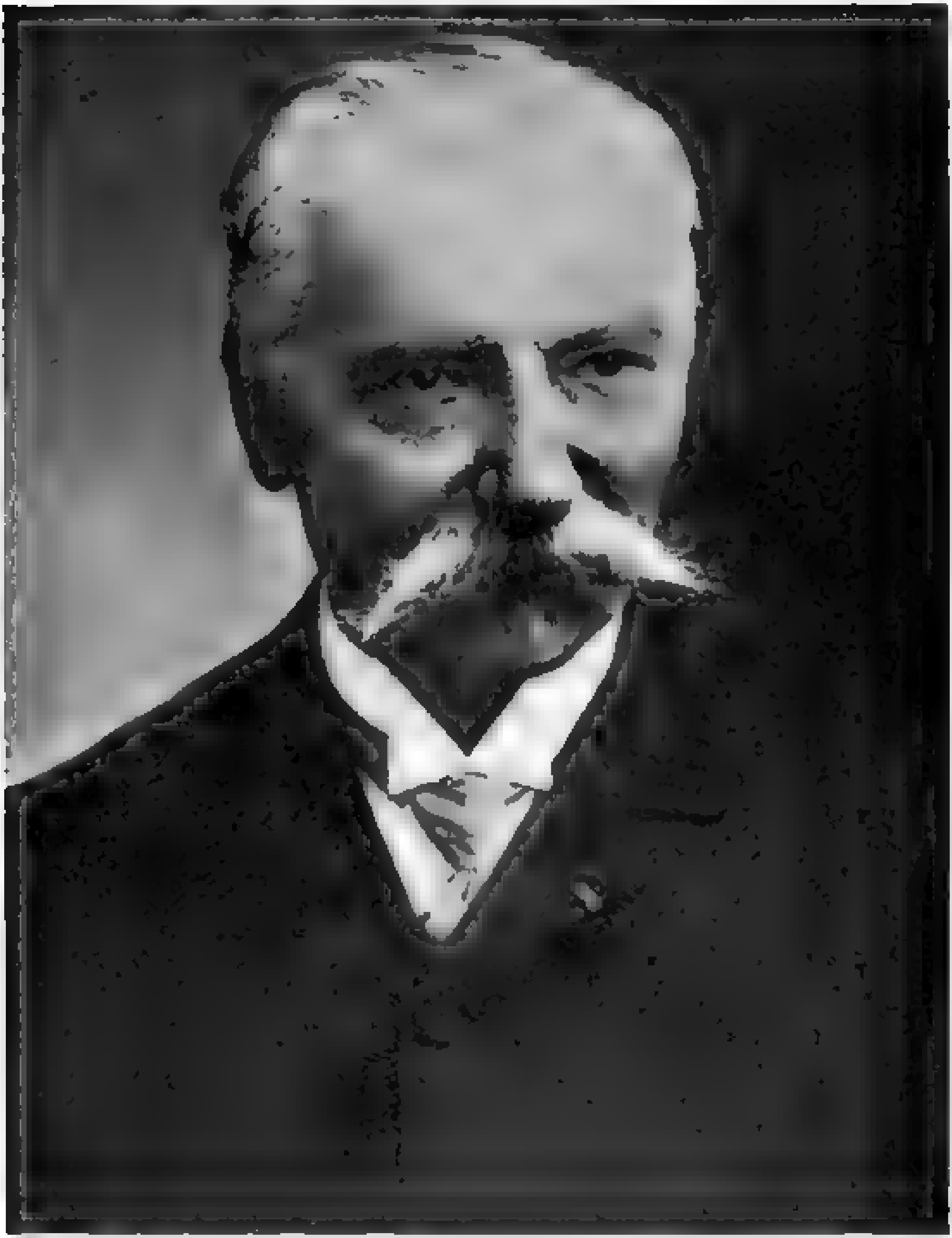
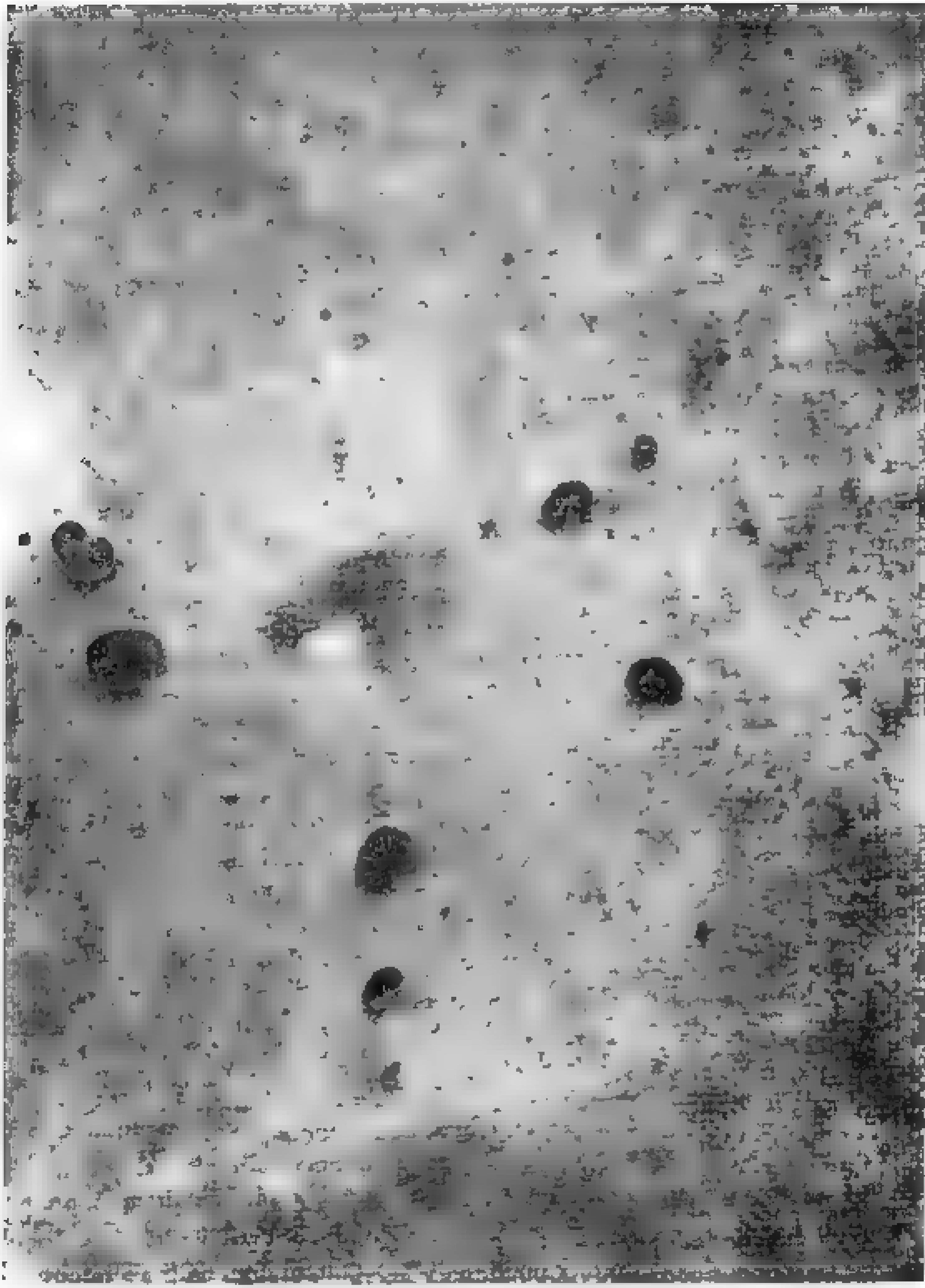


NARCISSE PATOUILLARD

(1854–1926)

Courtesy of the Director of the Laboratoire de Cryptogamie du Muséum National d'Histoire Naturelle, Paris, France

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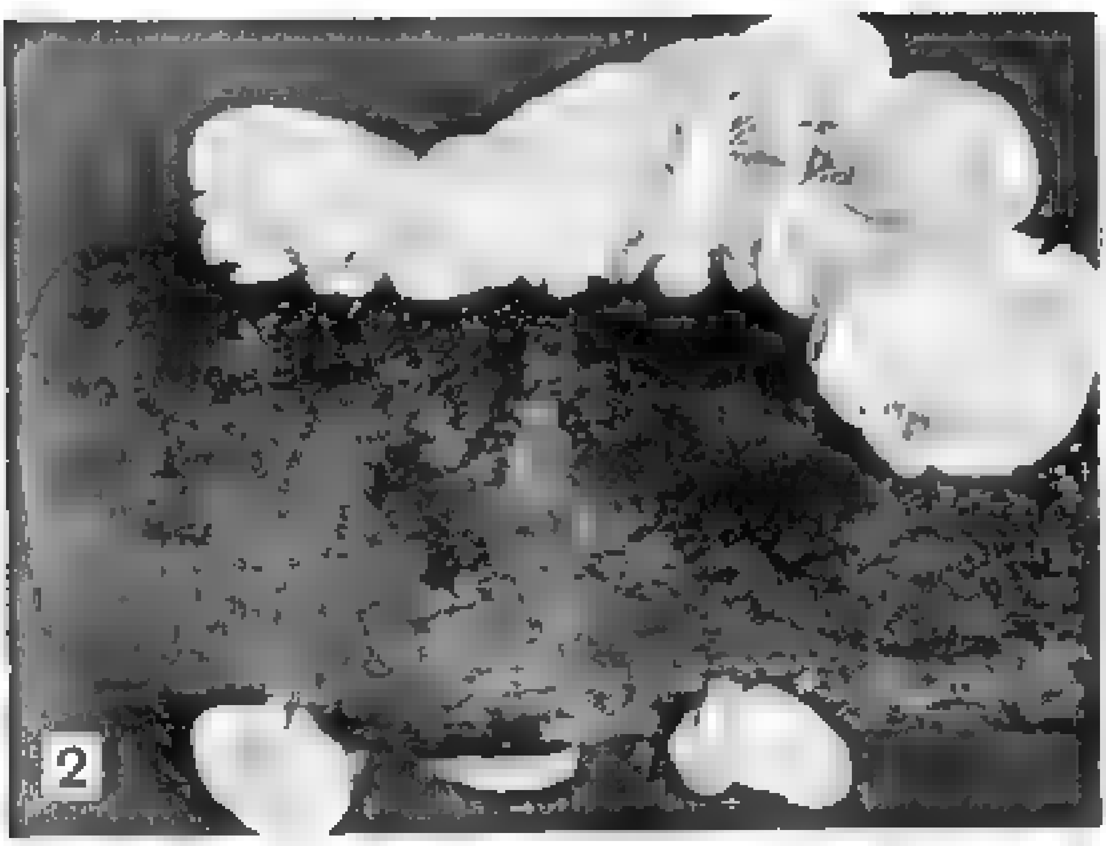
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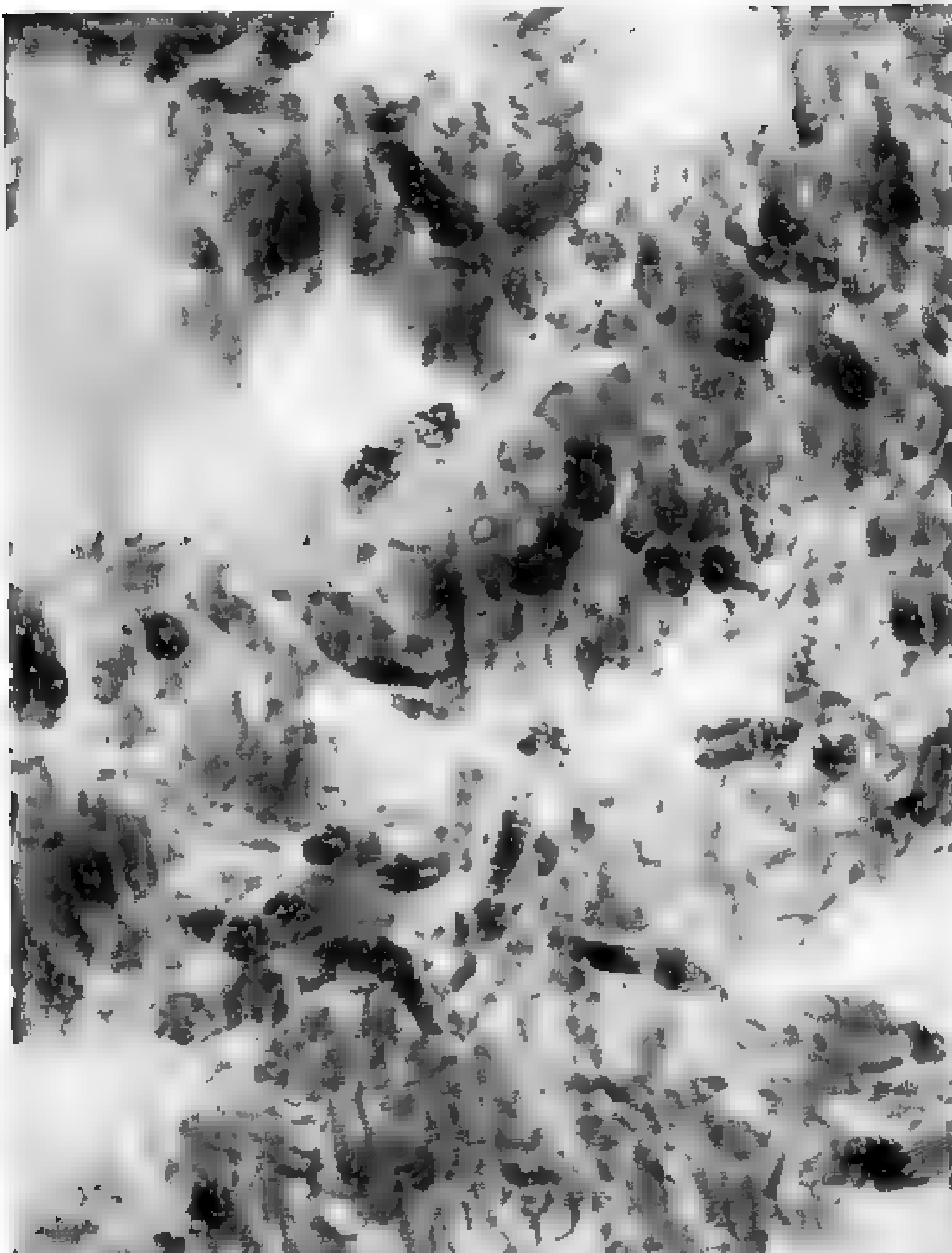

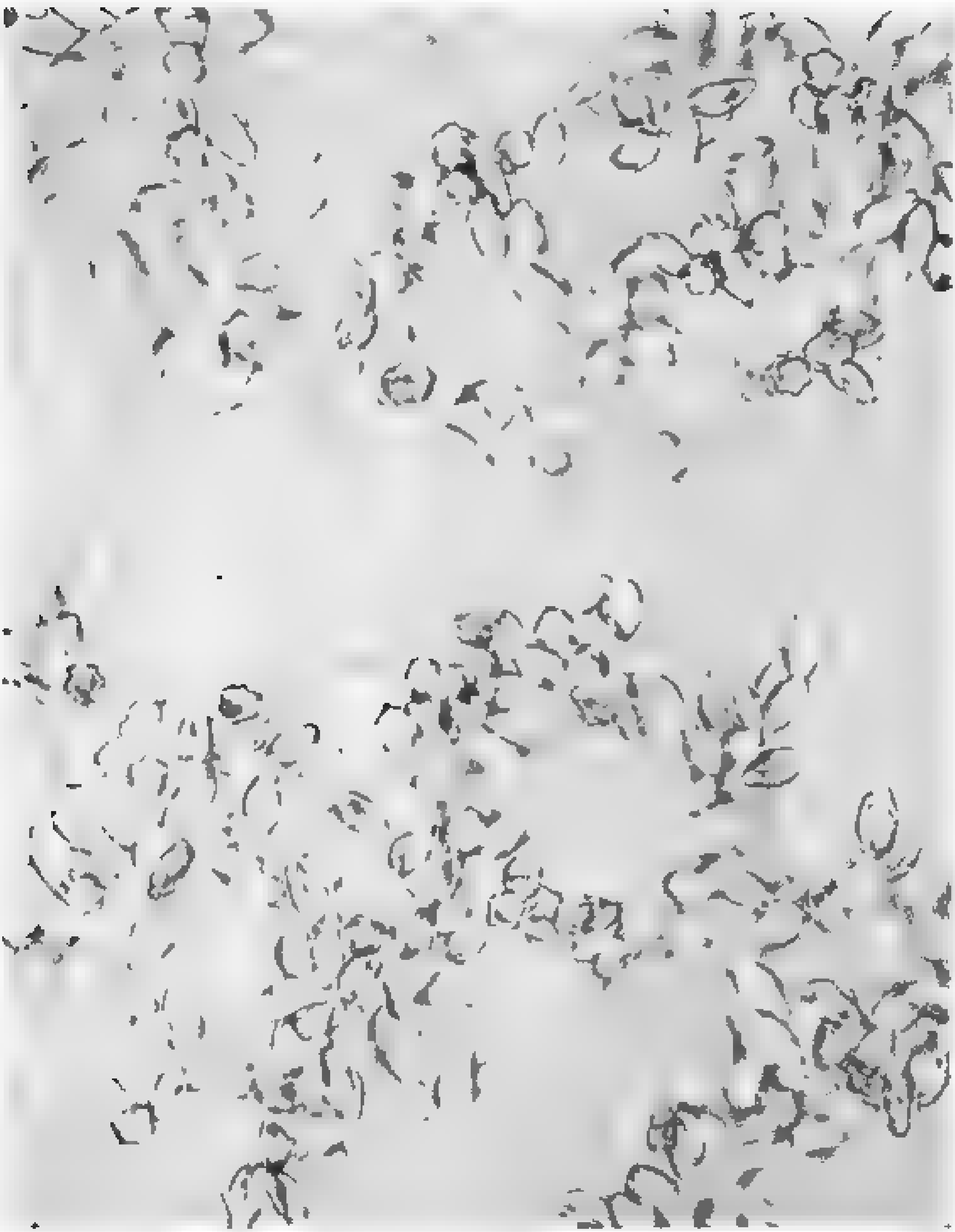

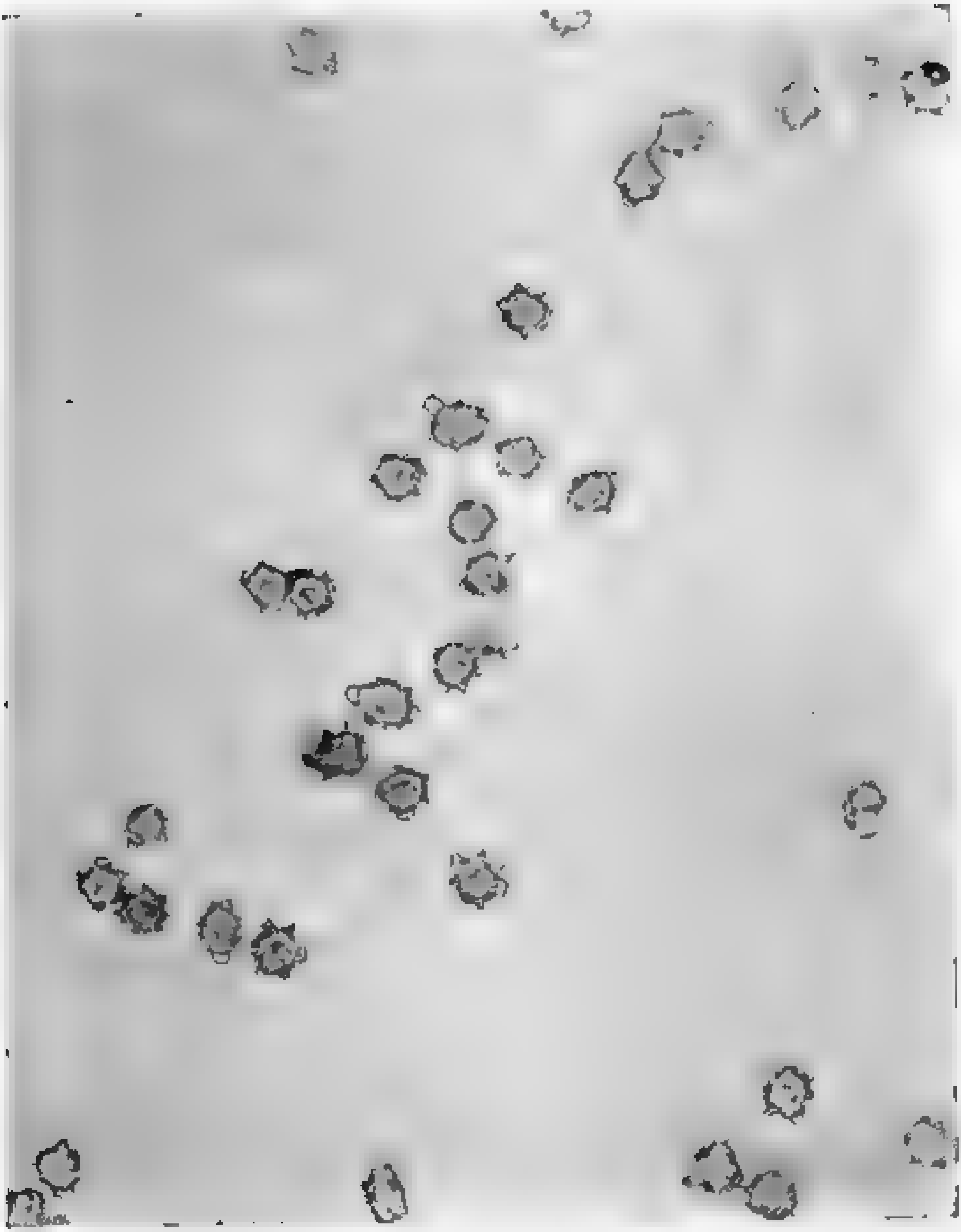

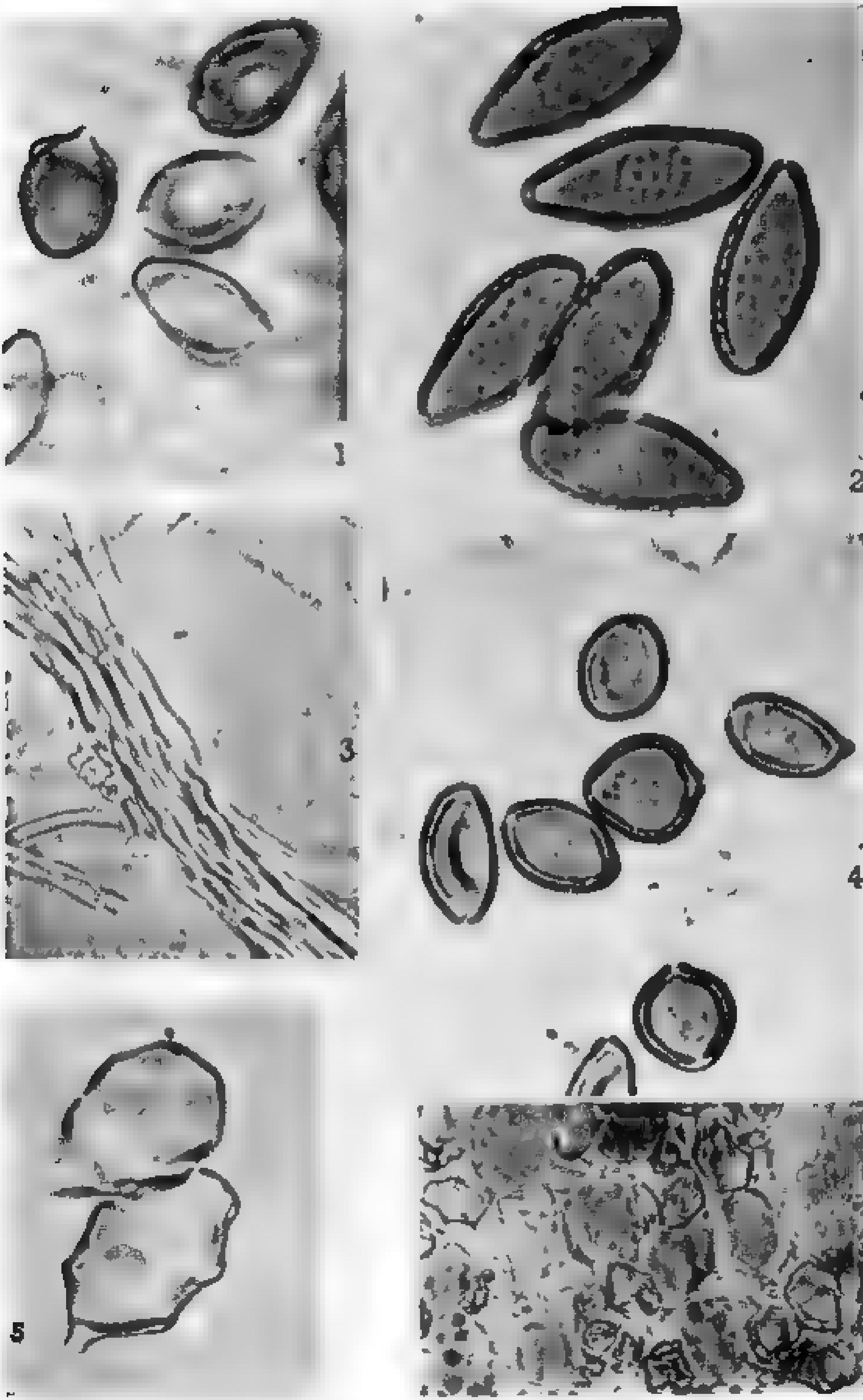
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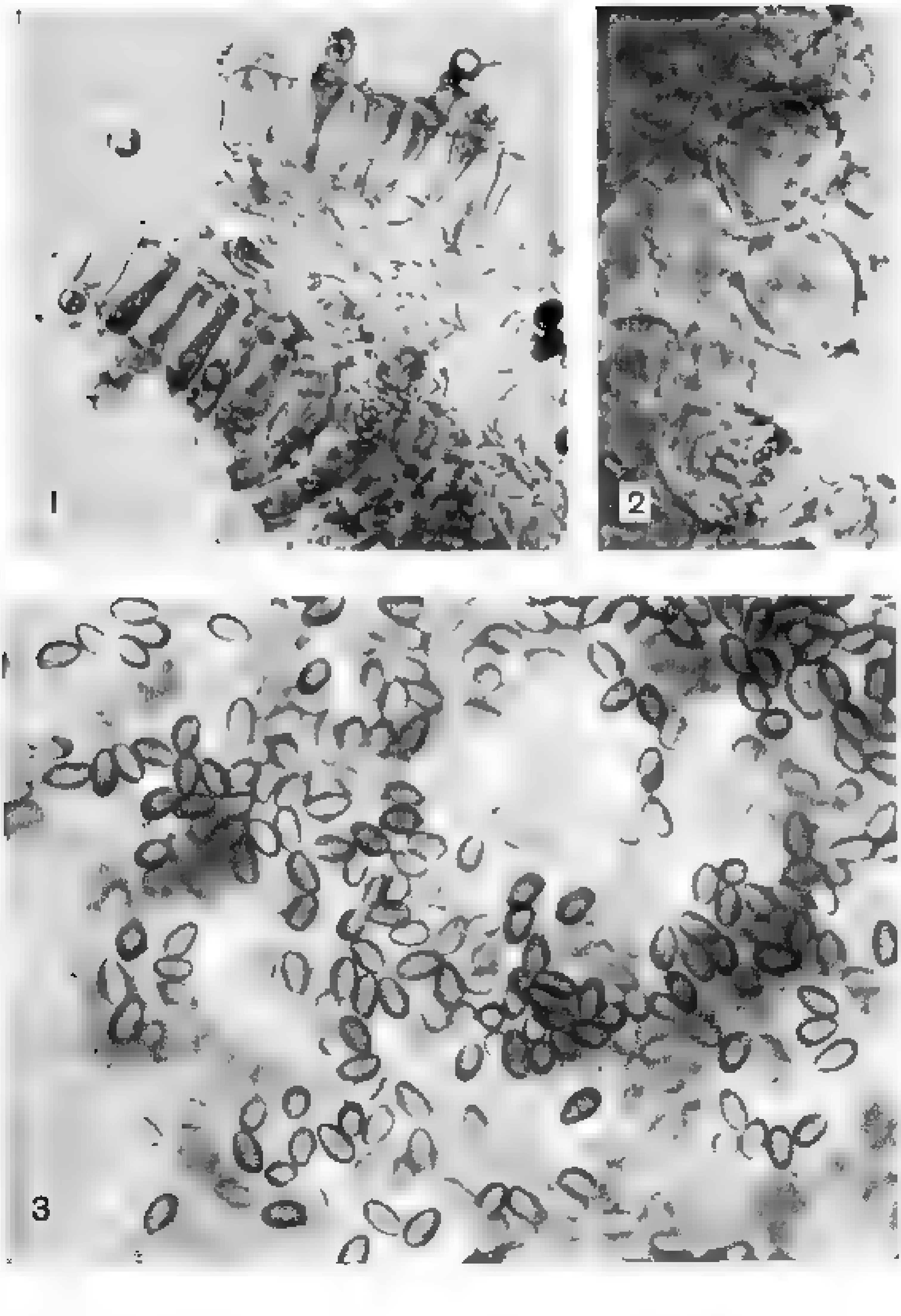

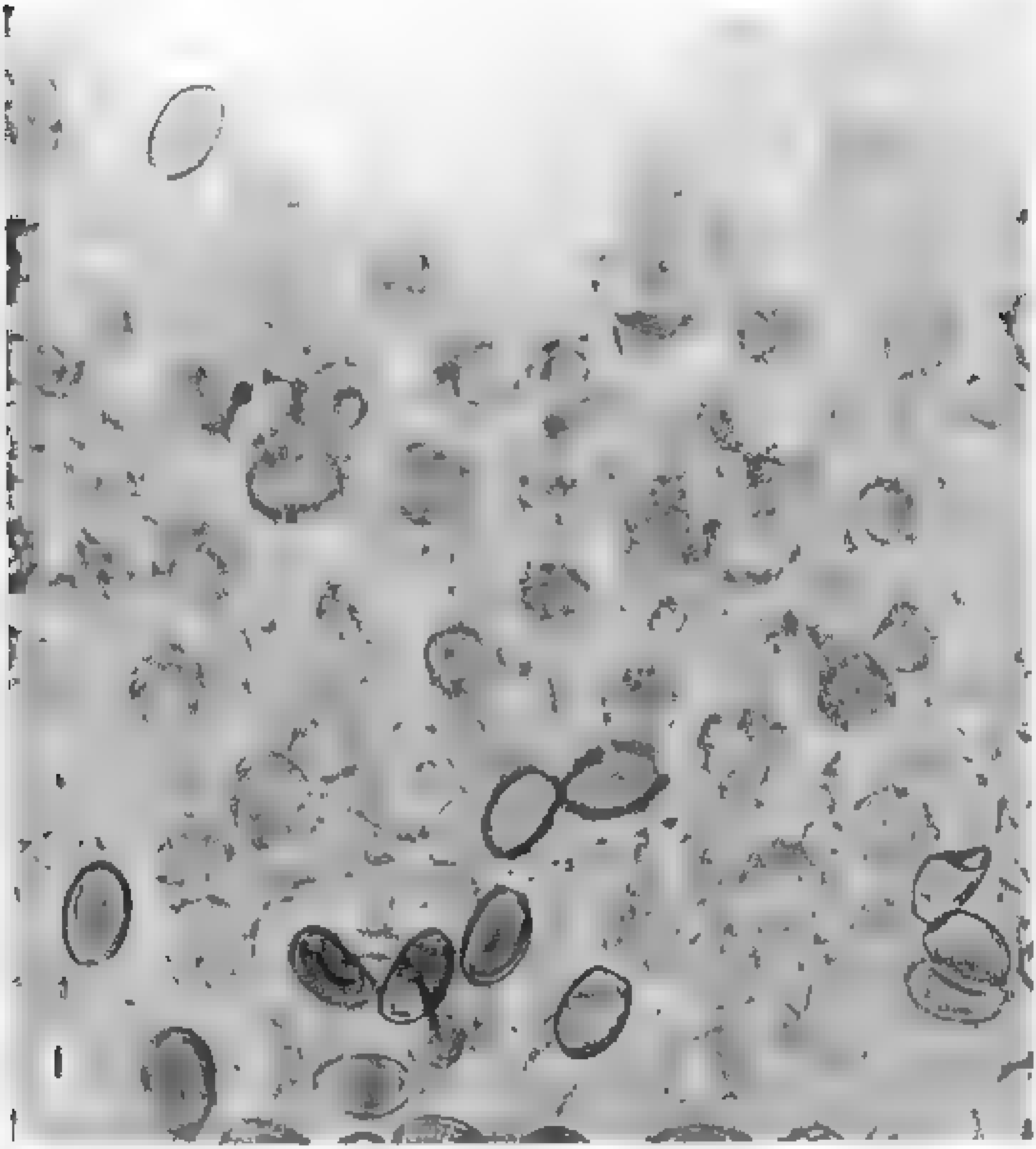

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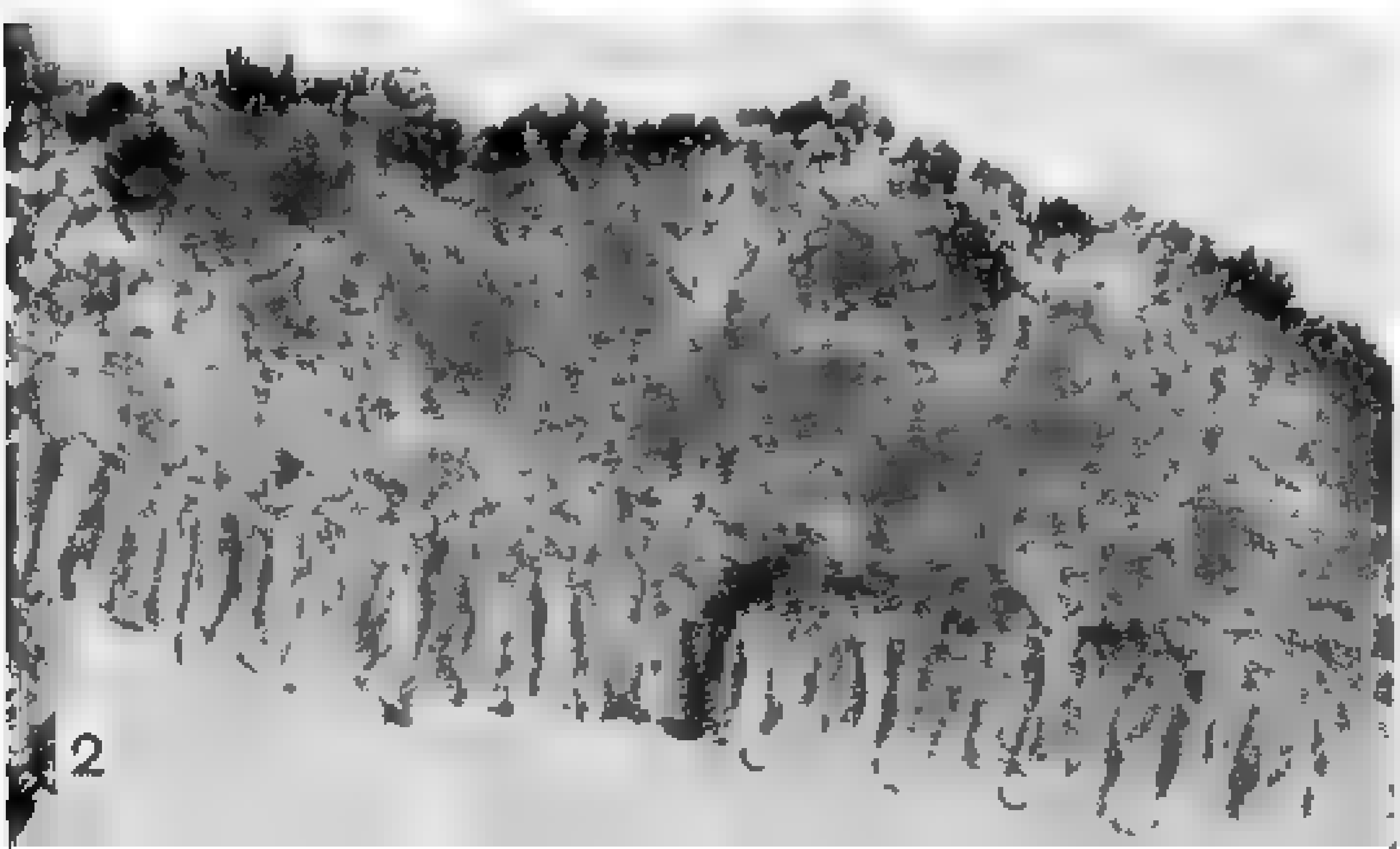

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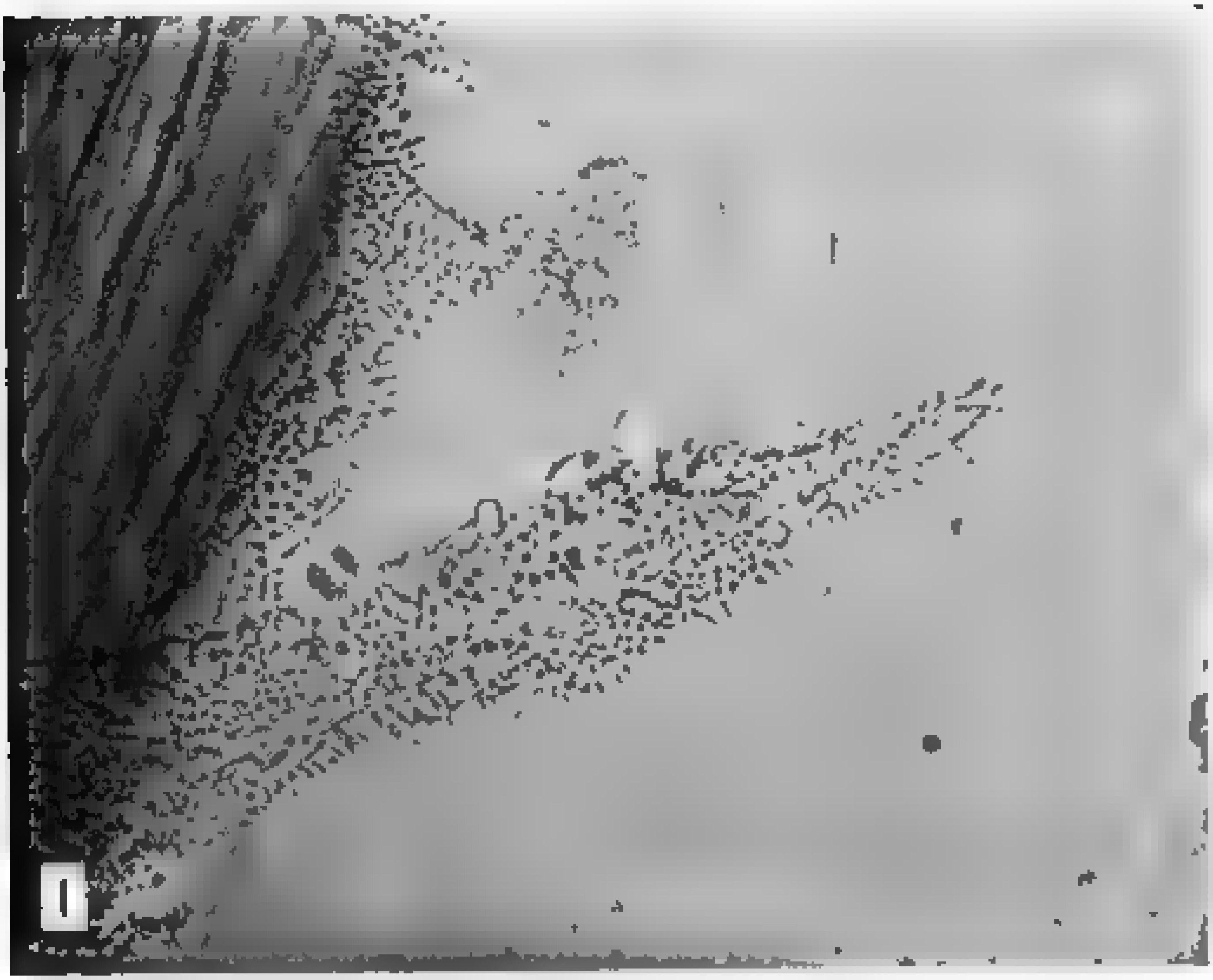
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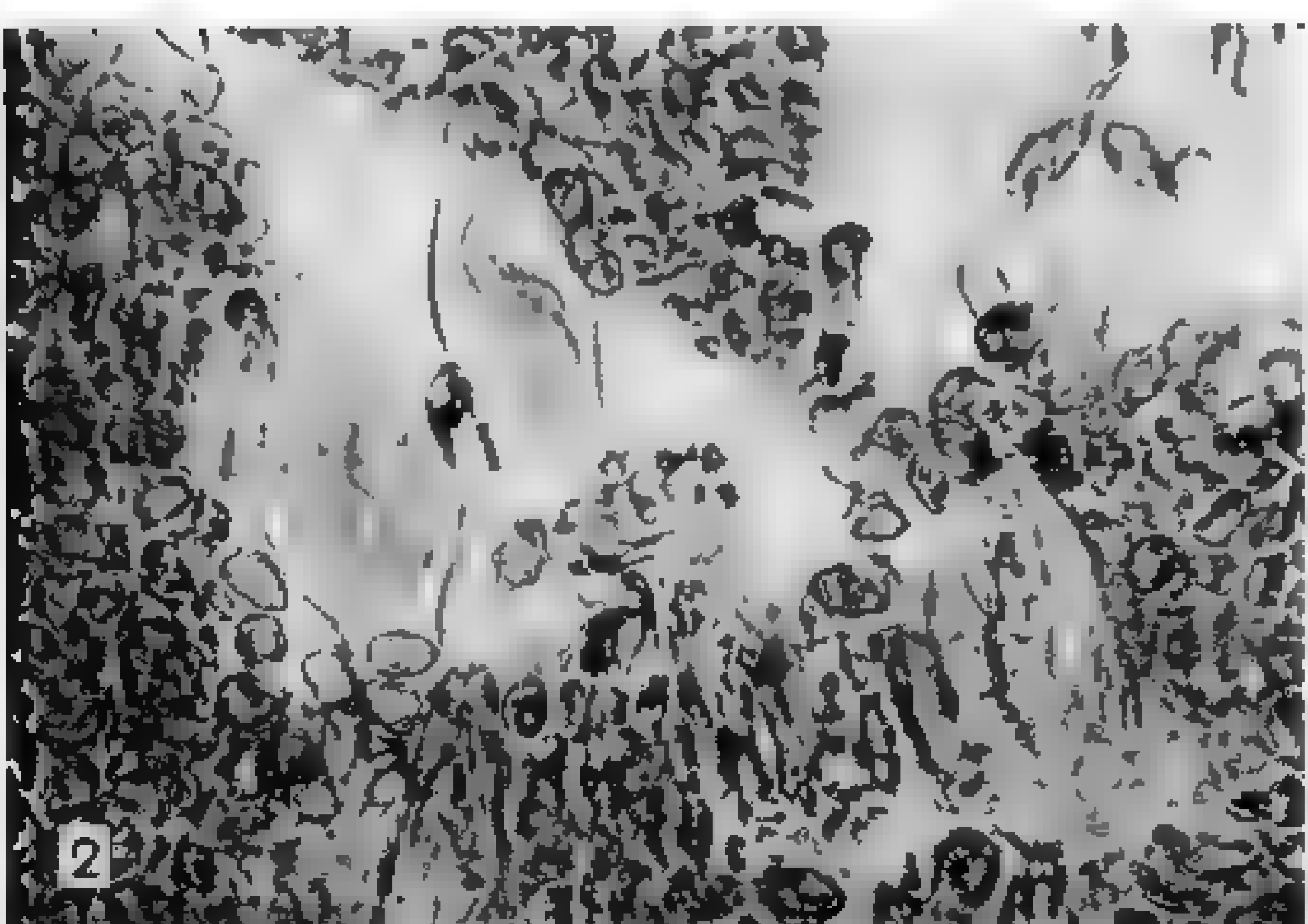
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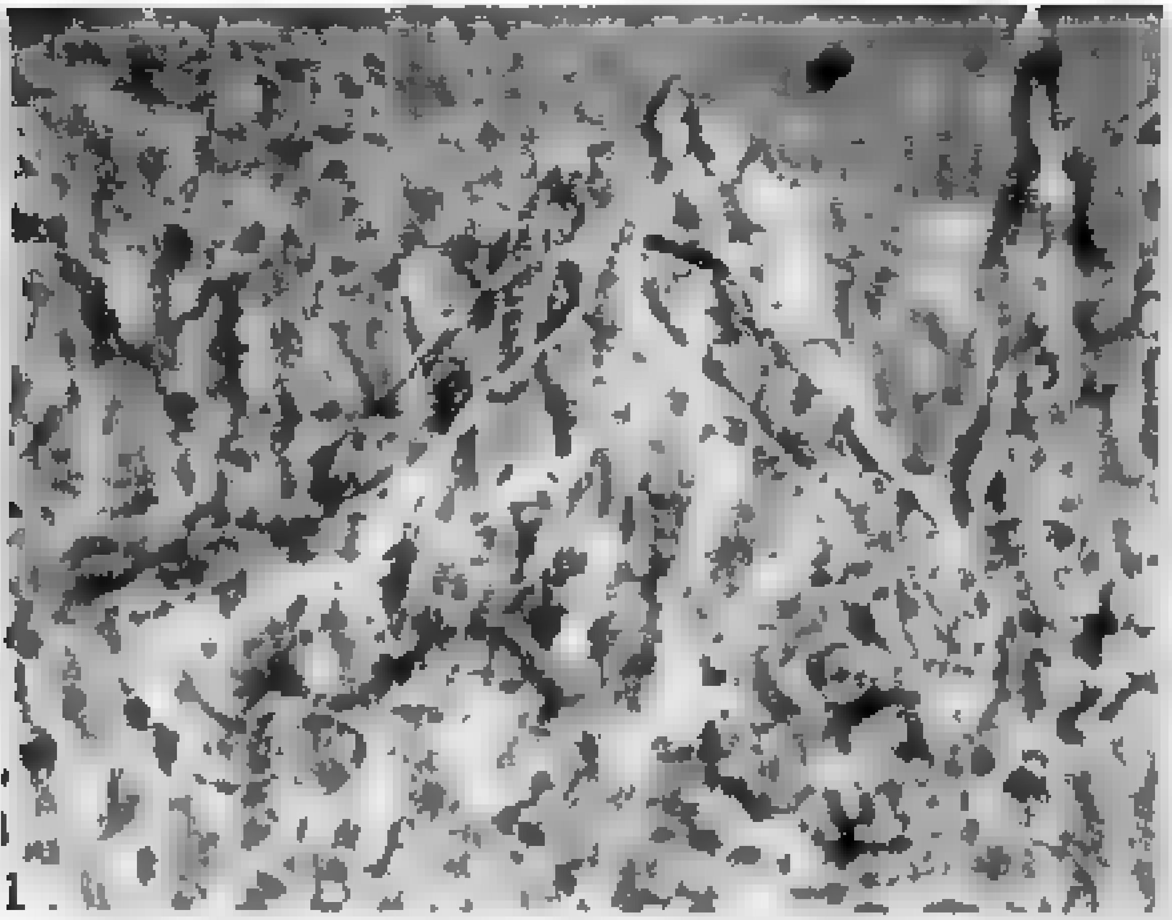

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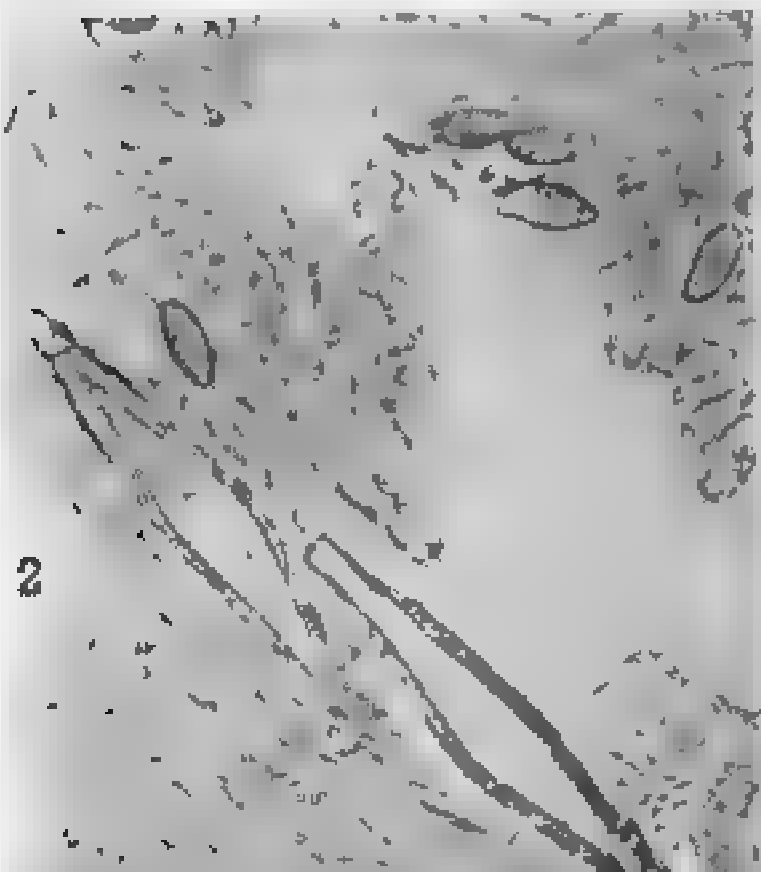

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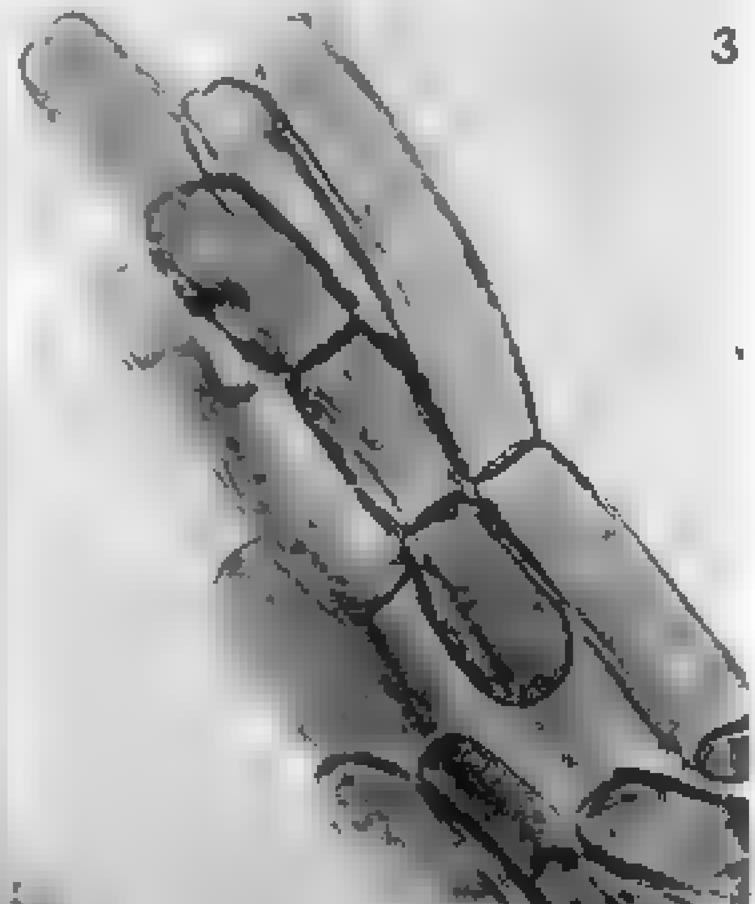

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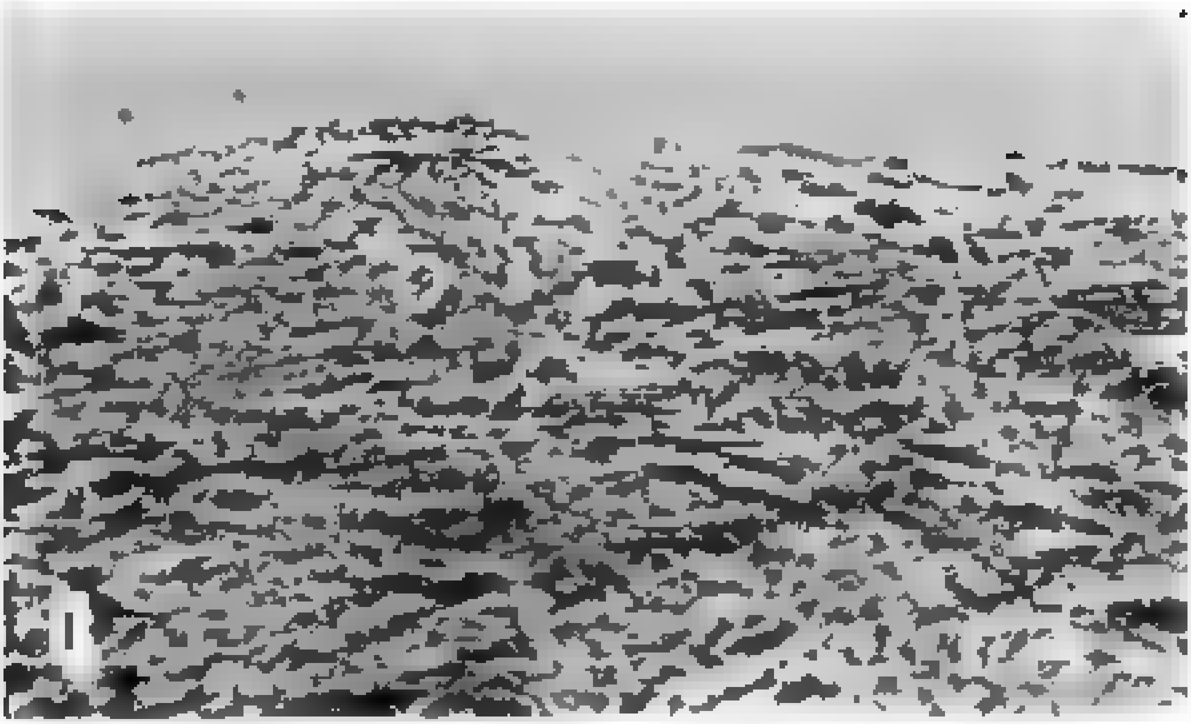
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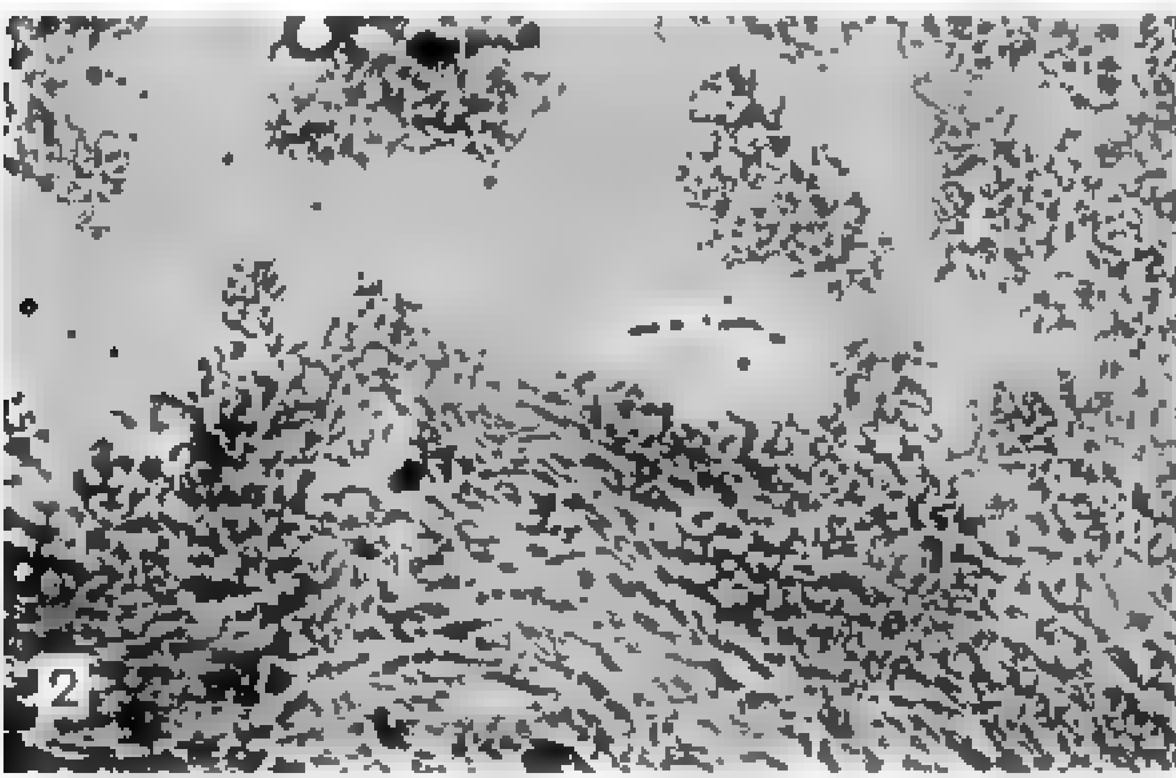
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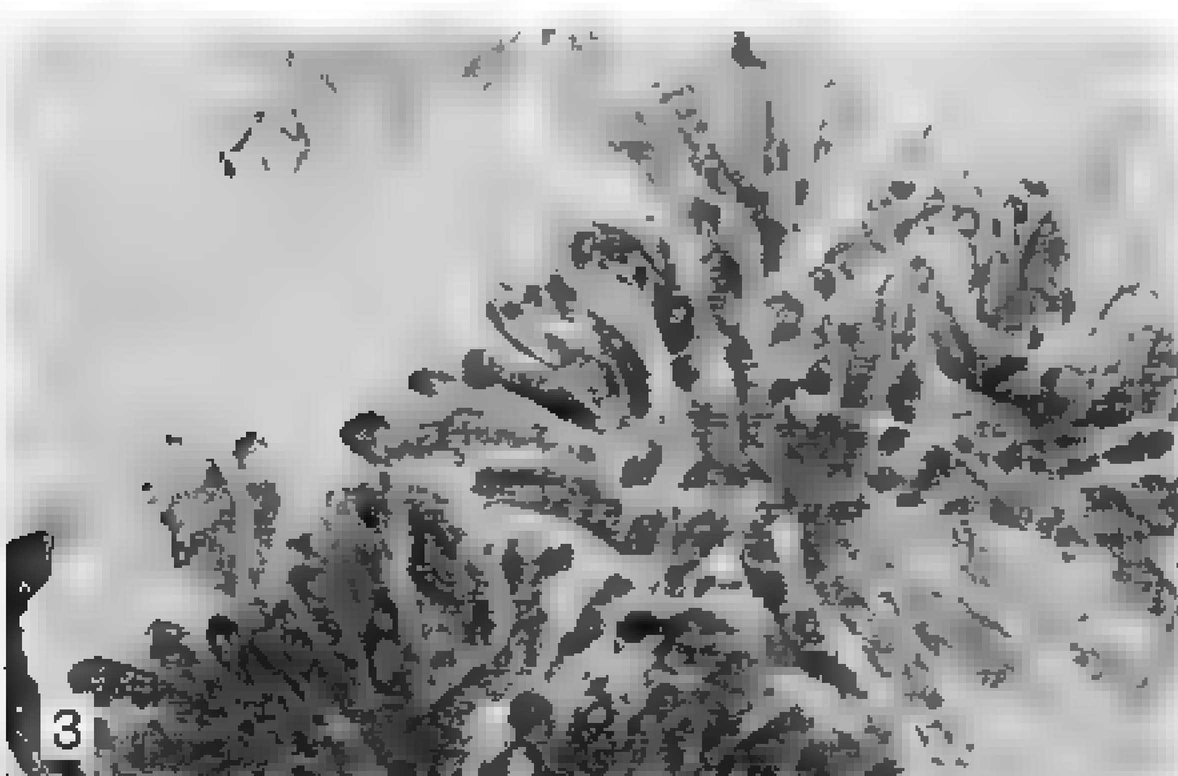
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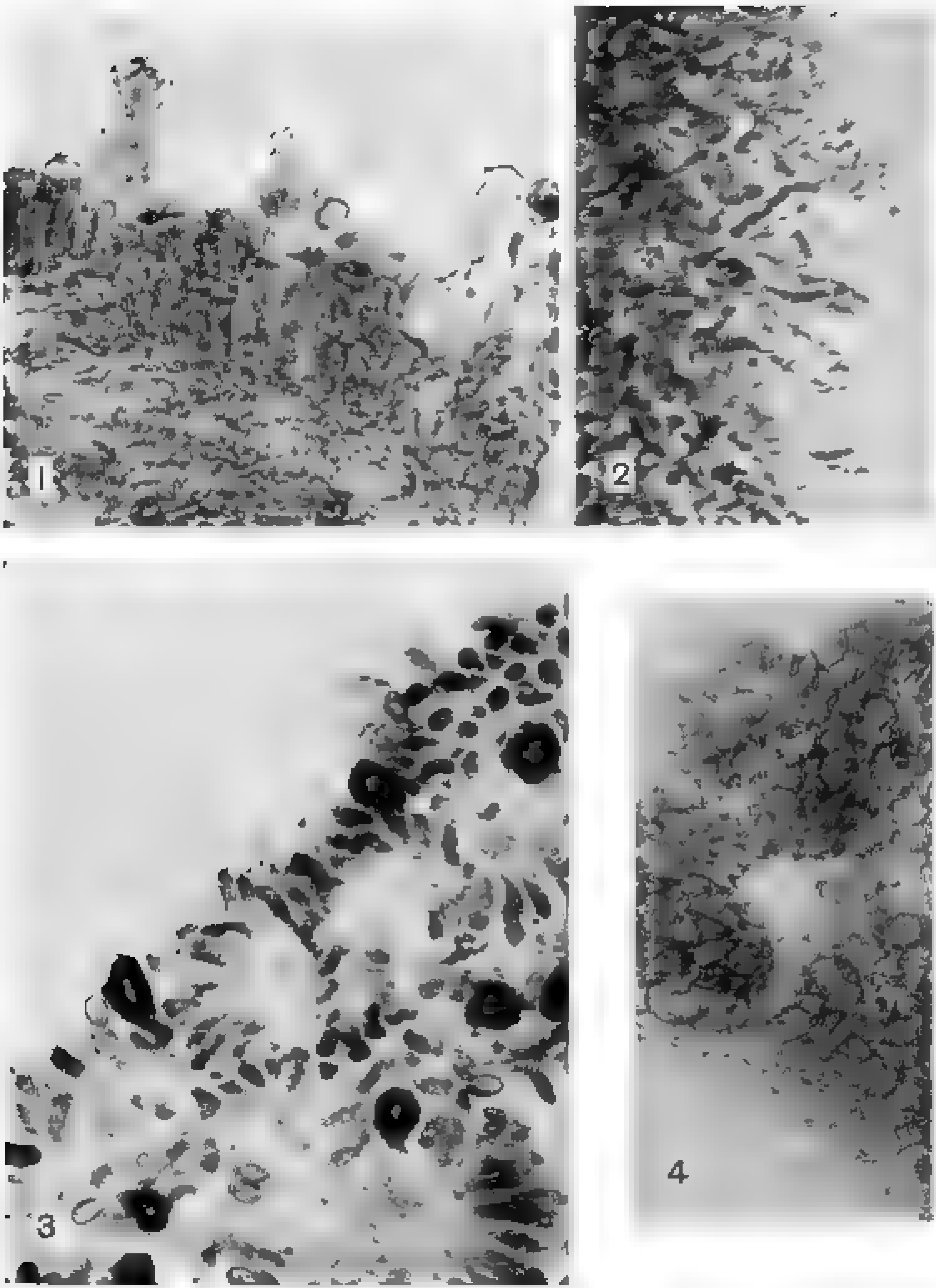
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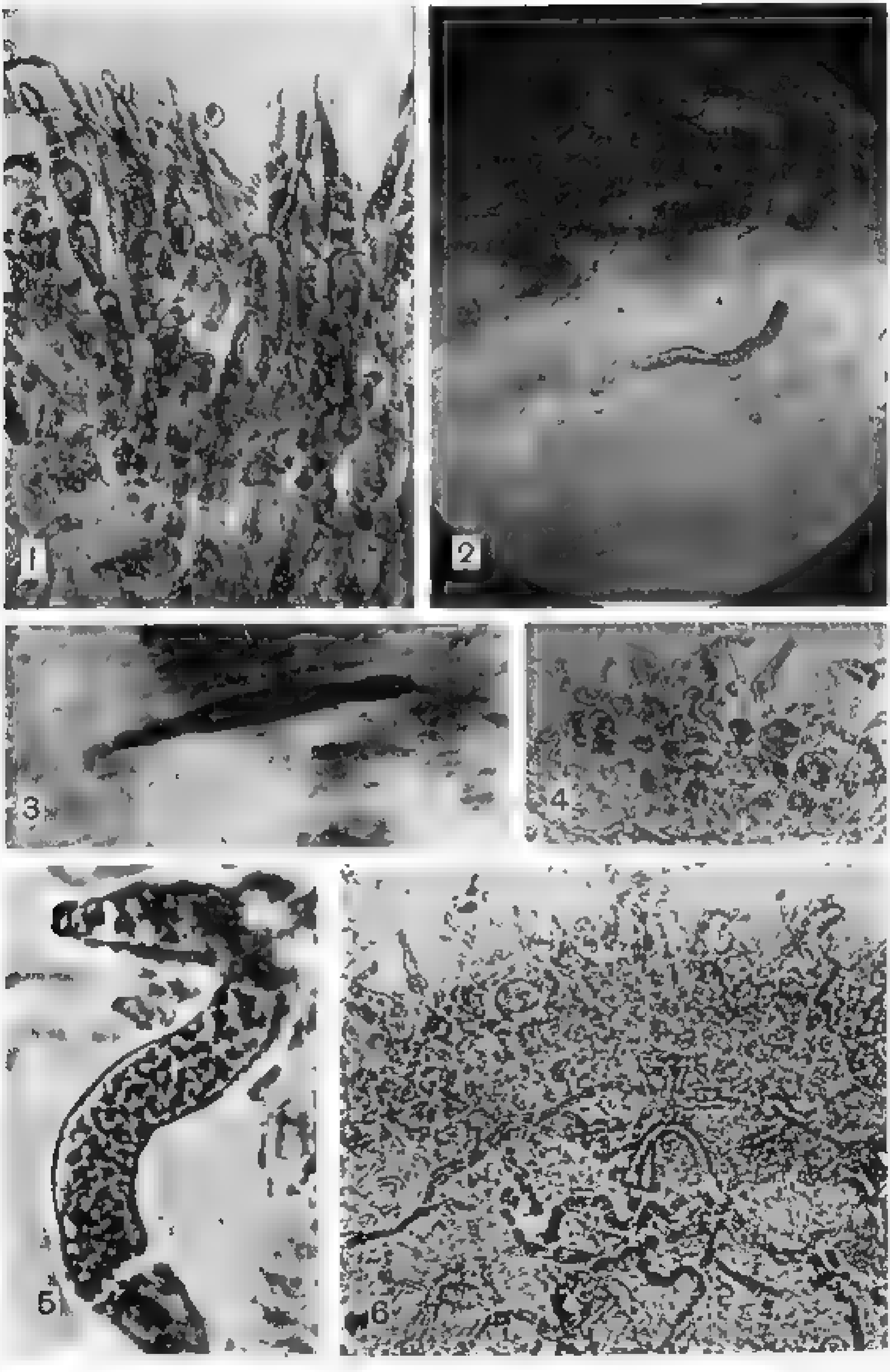
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EXPLANATION OF THE PLATES

If there is no statement to the contrary, the photographs were made by Mr. Frank White and the author in the Photographic Laboratory of the Biological Laboratories with a Spencer microscope from semipermanent slides of the author or from specimens determined by the author and preserved at the Farlow Herbarium. The drawings were prepared by the author, except for plate XXIII A (del. A. H. Smith) and plate XXIV (del. D. H. Linder), from specimens determined by the author, most of them preserved at the Farlow Herbarium.

PLATE I

Vincent Fayod, 1860-1900. Portrait from the Conservatoire et Jardin Botaniques, Geneva, Switzerland; copies purchased by the author and published with permission of the Director, Dr. Charles Baehni.

PLATE II

Narcisse Patouillard, 1854-1926. Courtesy of the Director of the Laboratoire de Cryptogamie du Museum National d'Histoire Naturelle, Paris, France.

PLATE III

Pleurotus tuber-regium (Woermann). Carpophores on pseudosclerotium. $\times 3/4$.

PLATE IV

Panus siparius. Carpophores on pseudosclerotium. Natural size.

PLATE V

Melanotus sp., probably *M. musaecola*. The mycelium damages fabrics, and fruits on this exposed gray duck in the American tropics (Panamá). Fresh specimens in natural size. Courtesy of Dr. D. H. Linder.

PLATE VI

Rhodophyllus abortivus. Normal fresh carpophores and carpophoroids in their natural habitat, about 3/4 natural size. Courtesy of Dr. D. H. Linder.

PLATE VII

Lampteromyces japonicus. Fresh specimens.

Fig. 1. In absolute darkness: the substratum is blacked out while the carpophores are luminescent enough to show on the film.

Fig. 2. The same group of carpophores in daylight, seen from below.

Fig. 3. Carpophores seen from above, in daylight. Courtesy of Dr. T. Hemmi.

PLATE VIII

Calocybe cyanella. Basidia with carminophilous granulation in aceto-carmine under oil immersion lens, × 1700.

PLATE IX

Clitopilus prunulus. Basidiospores in frontal view (fusoid), in profile (inequilaterally fusiform), and seen from one of the tips (longitudinal axis vertical: here seen as isodiametric angular to substellate bodies). Oil immersion lens, × 1000.

PLATE X

Asterophora lycoperdoides. Chlamydospores, × 480.

PLATE XI

Basidiospores of various *Agaricales*, and clamp connections.

Fig. 1. *Galerina Hypnorum* var. *ecelata.* Spores with a perisporium which is here persistent forming a smooth surface but sometimes loosened in an ear-shaped manner (spore at the left upper side), or becoming wrinkled (upper right) at maturity. Oil immersion lens, × 1800.

Fig. 2. *Porphyrellus subflavidus.* Spore ornamentation XI (heterogeneous spore wall). Oil immersion lens, × 1950.

Fig. 3. *Phyllotopsis nidulans.* Hyphae forming tomentum of pileus, with clamp connections. Oil immersion lens, × 700.

Fig. 4. *Deconica atrorufa.* Spores lentiform, with germ pore. The lowest spore in this figure, and also the central spore are seen frontally, and are very broad; their hilar point is on the geometric axis of the spore; the spores farthest to the left and farthest to the right are much narrower, as they are seen in profile with the hilar end outside the geometric axis; the two remaining spores of this figure are in an intermediate position. Oil immersion lens, × 1950.

Fig. 5. *Rhodophyllus squamifolius.* Angular spores, seen at strong magnification (× 1550) under oil immersion lens; the upper spore is in nearly frontal view.

Fig. 6. *Rhodophyllus squamifolius.* Angular spores of the symmetric type, loosely scattered on the surface of the hymenium; two spores in the right lower corner are in frontal view and show the angle of the hilar end at about 90°; the spore at left and one near the upper right corner are seen in profile, × 510.

Plate XII

Fig. 1. *Coprinus ebulbosus.* Section through the lamella showing the pavement-like arrangement of the pseudoparaphyses; the pseudoparaphyses are « empty », i. e. almost devoid of protoplasma to the point where phloxine does not dye them (consequently light colored in this photo); the basidia are of two sizes, one equalling the pseudoparaphyses but dark colored (in the preparation: red from the phloxine), the other strongly projecting (see upper side of lamella); note the thinness of the trama; black dots at right are spores. Oil immersion lens, × 605.

Fig. 2. *Marasmius rotula.* Section through the epicutis of the pileus (surface facing right side of the plate) with broom cells. Oil immersion lens, × 950.

Fig. 3. *Galerina marginata.* Spores with smooth spots, called plage (showing as a round white dot in those spores which have their inner sides turned toward the objetive); oil immersion lens, × 535.

Plate XIII

Fig. 1. *Bolbitius vitellinus.* Spores scattered on the surface of the hymenium; spores showing the germ pore at the apex and complex wall; hymenium showing the basidia (darker colored because richer in protoplasma and therefore dyed more strongly by phlo-

xiloe) and between them, the pseudoparaphyses (hardly colored, «empty»), both seen from above. Oil immersion lens, × 780.

Fig. 2. *Marasmius haematocephalus.* Erect elements with finger-like colored appendages form a hymeniform epicutis (uppermost layer of the pileus); underneath, the trama of the pileus and, then, the hymenium. This is a radial section of the pileus, × 570.

Plate XIV

Fig. 1. *Mycena osmundicola.* Longitudinal section through the outer layer of the stipe. Long, dendrophysoid hairs with echinate surface form the pubescence of the stipe and are here seen under oil immersion lens, in aceto-carmine medium, × 600.

Fig. 2. *Inocybe paludinella.* Crushed fragment of the lamellae with nodose spores; some metuloids visible, × 780.

Plate XV

Fig. 1. *Russula tenuiceps.* Section through the cuticle of the pileus; epicutis with clavate dermato-pseudocystidia of the macrocystidium-type showing the banded-granular (yellow) contents. Oil immersion lens, × 770.

Fig. 2. *Boletochaete brunneosetosa.* Two setuloid cystidia and spores of the Boletus-type. Oil immersion lens, × 650.

Fig. 3. *Rhodophyllus squamifolius.* Hair like hyphal strand of the pileus, consisting of parallel septate hyphae, × 375.

Plate XVI

Fig. 1. *Mycena permixta.* Radial section through the cuticle. The uppermost layer where the epicuticular hyphae are diverticulate; more voluminous hyphae are seen in the pigmented lower layer, the hypodermium. Oil immersion lens, × 460.

Fig. 2. *Asterotus dealbatus.* Above the loose hyphal trama of the pileus there is the dichophysoid cuticular layer which is here brutally disrupted by pressure in order to show the structure of the minute elements. Oil immersion lens, × 920.

Fig. 3. *Leccinum mutabile.* Hymenial fascicle of the tip of the scales of the stipe with a dermato-pseudoparaphysis (below) and a dermato-basidium (above), × 560.

Plate XVII

Fig 1. *Inocybe paludinella.* Metuloids with muricate apex and thick walls, ampullaceous in shape and rooting deep in the trama. Oil immersion lens, × 700.

Fig 2. *Trogia cantharelloides* Trichodermium (the surface of the pileus faces the right side of the plate), × 570.

Fig 3. *Stropharia aeruginea.* Chrysocystidia with a characteristic large body in the interior that becomes yellow in ammonia, and — as in this preparation — blue in cotton blue (or cresyl blue), i. e. a strongly contrasting black in black-and-white copies, × 570.

Fig 4. *Cystoderma fallax.* Epithelium of the pileus; the upper, darker portion, consisting of globose to subglobose cells, is the epithelium; in the lower left portion of the picture — the hyaline trama of the pileus; between the two layers a light colored hypodermium, consisting of small but short elements, × 225.

Plate XVIII

Fig. 1. *Russula terrotincta.* Section through the cuticle with an epicutis of erect ciliate dermatocystidia arising as terminal members from a subcuticular trichodermial palisade Oil immersion lens, phloxine-ammonia medium, × 450.

Fig. 2. *Amanita inaurata.* Section of the cuticle, the upper, darker zone is the volval layer of the young carpophore, beneath it the cuticle proper with an oleiferous hypha (dyed with phloxine), volval layer consisting of numerous isodiametric elements and connective hyphae; cuticle proper somewhat gelatinized and hyphae loosely arranged, × 290.

Fig. 3. *Lactocollybia cycadicola.* Gloeo-vessel in the trama On the slightly colored background of ordinary hyphae, the gloeo-vessel appears almost black (deep blue in cresyl blue). Oil immersion lens, × 630.

Fig. 4. *Lactarius nigroviolascens.* Radial section through the cuticle, showing the « Virescens-structure » which consists of dark (pigmented) spherocysts from which ciliate dermatocystidia arise forming the epicuticular layer, × 285.

Fig 5 *Linderomyces lateritius* Coscinoid, first treated with KOH, then dyed with phloxine Oil immersion lens, × 1200.

Fig. 6 *Lactarius nigroviolascens.* A section through the cuticular region of the pileus, the lower portion showing the hyaline trama of the context with numerous worm shaped laticifers, the upper portion showing the « Virescens structure », × 285.

PLATE XIX

Fig 1. *Hohenbuehelia angustata*. Gelatinous layer, consisting of loosely arranged hyphae imbedded in a gelatinous mass (light zone); above it, the cuticular zone which is of the « dense » type facing the left upper corner), beneath (lower right half of the figure) the non-gelatinized portion of the trama of the pileus, 290

Fig. 2. *Russula Puiggarii*. Spores in Melzer's reagent, showing the reticulate ornamentation (type I), the exosporial layer of the spore wall turning blackish lilac in this medium; the spores are almost perfectly globose and belong to a nearly orthotropic type; × 620.

Fig. 3. *Boletochaete brunneosetosa*. Brownish seta-like cystidia with transitions toward hyaline cystidioles (immediately to the left and partly underneath the seta-like body) Oil immersion lens, × 680.

Fig. 4. *Conocybe siliquea*. Capitate cheilocystidium Oil immersion lens, × 1550.

Fig 5. *Russula tenuiceps* Intermixed trama (heteromerous), the spherocysts predominant, but some fine filamentous connective hyphae also visible, × 640.

PLATE XX

Fig 1. *Lactarius coleman* var. *corrugis*. Section through the pileus near the margin; innumerable dermatocystidia forming the palisade of the cuticular layer of the pileus, numerous laticifers in the context, numerous cystidia in the hymenium; the section of the lamellae showing the characteristic wedge-shaped outline of the majority of the agarics. The trama of the lamellae not predominantly vesiculose. Magnification about 50 ×.

Fig 2. *Chamaeota sphaerospora* Inverse hymenophoral trama The edge of the lamella is in the direction of the lower right corner, the hyphae of the trama are divergent but in an inverse manner, away from the edge, × 425.

Fig. 3 *Crepidotus mollis*. Section through the pileus, with the cuticle (denser darker layer above), the gelatinized zone (loosely arranged zone beneath the cuticle), the non gelatinized zone of the context (denser narrower portion beneath the gelatinized zone), and, finally the deeply colored (in phloxine) hymenial layer, × 100.

Fig 4. *Coprinus micaceus*. Section of the pileus and the hymenophore near the margin. The lamellae are as broad or narrower in their upper

portion than in the middle, they are also thinner and closer when compared with fig. 1 of this plate (*Lactarius volemus* var. *corrugis*), autodigestion has not begun yet. Note the vesiculose cystidioles on the left hymenium of the second (from the left) lamella and on other points of the hymenia (some have been torn loose by the separating lamellae 1 and 2 and are floating in the medium, × 60.

Plate XXI

Fig. 1. *Pleurotus levis.* Section through the lamella (edge beyond the lower margin of figure); first treated with KOH, then neutralized, and first dyed with phloxine which for contrast is replaced by cotton blue in the trama and the hymenium while the subhymenium remains pink (light colored in contrast to the dark colored blue portion if a yellow filter is used): the distinct broad subhymenium and the irregular trama are characteristic for the genus *Pleurotus*, × 90.

Fig. 2. *Conocybe siliginea.* Section through the lamella. The voluminous cells of the hypodermium of each corresponding side of the lamella almost touching each other, with the trama proper (fine filamentous hyphae) strongly reduced, × 260.

Fig. 3 *Lactocollybia cycadicola.* Gloeocystidium. Short exposure of the copy makes the granulosity of the interior show: the interior is dark because of the blue color it assumes in cresyl blue stains. Oil immersion lens, × 640.

Fig. 4. *Melanoleuca* sp. (NY-234) Cystidiole in cresyl blue, metachromatic in cresyl blue; the wall is purplish, and part of the context is also colored; the basidia (here black) are very deep violet in the original slide Oil immersion lens, × 920.

Fig. 5. *Panus rudis* var. *strigellus* Section of the lamellae (edge toward right lower corner), showing a completely irregular structure and absence of a subhymenium although treated exactly like the preparation shown in fig. 1 (*Pleurotus levis*), hymenium was deep blue, trama light blue, × 175.

Plate XXII

Fig. 1. *Boletellus Russellii.* Section through the young hymenophore, showing the bilateral (*Boletus* type) structure of the tube walls, the mediostratum in the middle of the tube wall is darker colored (though not stained), the lateral stratum is divergent; the pores

are in the direction of the lower right corner. Leitz dry objetive, × 395.

Fig. 2. *Hohenbuehelia angustata.* Section through the hymenium, with a metuloid, deep-rooting and thick-walled, × 475.

Fig. 3 *Hygrocybe cuspidata.* Section through the lamella, showing the strictly regular structure of the hymenophoral trama; the hymenium on the left side partly broken off. 180.

Fig. 4 *Pluteus cervinus.* Characteristic horned tip of metuloid (pleurocystidium) in phloxine stain Oil immersion lens, × 900.

Plate XXIII

Fig. A. Anatomical details of *Leucopaxillus.*

1. Spores of *Leucopaxillus laterarius.*
2. *L. albissimus.*
3. *L. giganteus.*
4. *L. tricolor.*
5. *L. amarus.*
6. *L. pulcherrimus.*
7. Hyphae from the cuticle of *L. amarus* f *typicus.* Drawn with the help of a camera lucida by A H Smith, magnification approximately 1485 ×.

Fig. B. Anatomical details of *Kuehneromyces* and *Pleuroflammula.*

1. *Kuehneromyces depauperatus,* cheilocystidium.
2. *K mutabilis,* spore in approximately frontal view, the outer black line showing the episporium, the inner thin line representing the endosporium's inner surface and the inner surface of the outer black line its outer surface touching the episporium; broad germ pore at the apex.
3. *K. mutabilis,* four cheilocystidia; at the right is a cheilocystidium showing a drop of mucilage at the apex
4. *Pleuroflammula Dussii,* cheilocystidium.
5. *Pl. Dussii,* spore; the outer black line represents the episporium, the inner black line, the bright and deep colored ring inside the endosporium; the white zone between the two lines is the endosporium proper; germ pore extremely narrow.
6. *Kuehneromyces rostratus,* two cheilocystidia.
7. *K. vernalis,* five cheilocystidia in the middle representing the common type I; these are flanked by cheilocystidia of type II. All drawings about 1175 ×, except for 2 and 5 which are magnified approximately 2700 ×.

Plate XXIV

Anatomical details of the *Strobilomycetaceae*. All drawings are made with the aid of a camera lucida from dried material mounted in KOH phloxine (basidia and cystidia) or either ammonium hydroxide or Melzer's reagent (spores) under oil immersion lens. Magnification approximately × 1050.

Fig. 1. *Strobilomyces confusus* Sing. Spores, basidium; from the type specimen.

Fig. 2. *Strobilomyces floccopus* (Vahl ex Fr.) Sacc. Spores, basidium; specimen from Harvard, Massachusetts.

Fig. 3. *Boletellus turbinatus* (Snell) Sing. Spores, basidium; from the type specimen.

Fig. 4. *Porphyrellus subflavidus* (Murr.) Sing. Spores; from authentic material.

Fig. 5. *Porphyrellus gracilis* (Peck) Sing. Spores, basidium; from authentic material.

Fig. 6. *Strobilomyces velutipes* Cooke. Spores, basidium; from the type material.

Fig. 7. *Boletellus ananas* (Curt.) Murr. Spores, basidium; specimen from North Florida.

Fig. 8. *Strobilomyces pterosporus* Sing. Spores, basidium; from the type specimen.

Fig. 9. *Boletellus Russellii* (Frost) Gilb. Spores, basidia and cystidia.

Fig. 10. *Boletellus Lauderi* Sing. Spores, basidium; from the type specimen.

Plate XXV

Anatomical details of the *Boletaceae*. All drawings of spores are at a magnification of × 2000; all other drawings of microscopic structures at × 1000; figs. 5-7 shown at natural size.

Figs. 1-4. *Gyroporus purpurinus* (Snell) Singer.

1. Structure of the cuticle of the pileus.
2. Cheilocystidia of the hymenophore.
3. Basidium.
4. Spore.

Figs. 5-7. *Boletinus decipiens* (B. & C.) Peck.

5. Gastromycetous conditions of the carpophore sketched at natural size.

6. Longitudinal section of an immature carpophore (natural size). The veil closely applied to the surface of the hymenophore.
7. Longitudinal section of a mature carpophore (natural size), the remnant of the veil remaining as a relatively closely attached annulus.

Figs. 8-10. *Suillus cothurnatus* ssp. *thermophilus* Singer.

8. Part of the hymeniform fragments on the surface of the stipe that are found in and around the glandular dots.
9. Large dermatocystidia, another element of the glandular dots of the stipe.
10. Spore.

Figs. 11-12. *Phylloporus rhodoxanthus* ssp. *foliiporus* (Murr.) Singer.

11. Spores.
12. Cystidia of the hymenophore.

Plate XXVI

Anatomical details of the *Boletaceae*.

Fig. 1. *Boletus edulis* Bull. ex Fr. Structure of the epicutis, × 1000.

Fig. 2. *Boletus aereus* Bull. ex Fr. Structure of the epicutis, × 1000.

Fig. 3. *Boletus rubellus* Krombh. ssp. *fraternus* (Peck) Sing. Structure of the epicutis, × 1000.

Fig. 4. *Boletus granulosiceps* Sing. Structure of the epicutis × 1000.

Fig. 5. *Boletus subsolitarius* Sing. Fragment of the hymenial layer on the margin of the pileus, × 1000.

Fig. 6. *Leccinum albellum* (Peck) Sing. Cystidium of the hymenophore, × 1000.

Fig. 7. *Leccinum albellum* (Peck) Sing. Epithelium of the pileus. The broken line above indicates the surface of the pileus, × 1000.

Fig. 8. *Xanthoconium stramineum* (Murr.) Sing. Spores, × 1000.

Fig. 9. *Boletus peruanus* Pat. & Baker. Section through the fresh carpophore in natural size. From a drawing accompanying the type specimens; del. C. F. Baker.

Plate XXVII

Anatomical details of *Gomphidius* and *Chroogomphus*. All figures are drawn at a magnification of × 2000.

Figs. 1-3. *Gomphidius rutilus* (Fr.) Lund. & Nannf. ssp. *alabamensis* (Earle) Singer.

1. Cystidium.
2. Basidium.
3. Two spores (left) frontal view : (right) in profile

Figs. 4-7. *Gomphidius viscicolor* Peck ssp. *jamaicensis* (Murr.) Sing.
4. Two spores, (left) nearly-frontal view : (right) in profile.
5. Hyphae of the remainders of the veil on the apex of the stipe, running in parallel strands, with strong pigment-incrustation.
6. Basidium.
7. Cystidium with the partially thickened wall.

Figs. 8-11. *Clitopilus scyphoides* (Fr.) Sing. var. *floridanus* (Murr.) Singer.
8. Two spores, (above) in frontal view ; (below) in profile with the hilar end above ; the line A...B indicates the longitudinal axis, C...D the short axis.
9. Three spores, seen from above (the longitudinal axis A...B vertically directed toward the lens), the short axis indicated corresponding to fig. 8, lower spore, as C...D. The upper spore shows 6 flattened sides and 6 angles, central one 7, the lowest 8 (which is the normal number in this form).
10. Basidium.
11. Hyphae of the sericeous covering of the pileus.

PLATE XXVIII

Anatomical details of *Crinipellis* and *Chaetocalathus*.

Fig. 1. Showing the hairs of the pileus of seven species of *Crinipellis*, × 450.
a. *C. stupparia*. Base of hair in connection with the hyphae of the hypotrichium, and upper part of a hair.
b. *C. mirabilis*. Upper part of three hairs from the pileus.
c. *C. carecomoeis* var. *Litseae*. Upper part of three hairs from the pileus.
d. *C. stipitaria* var. *graminealis*. Upper part of two forked hairs from the margin of the pileus.
e. *C. septotricha*. Upper part of three ladder-like hairs of the pileus.
f. *C. excentrica*. Upper part of three appendiculate hairs of the pileus.
g. *C. chrysochaetes*. Pseudoamyloid bodies of the epicutis of the pileus.

Fig. 2. Showing different elements of the hymenium of *Crinipellis*, × 450.
a. *C. carecomoeis* var. *Litseae*. Basidia, some of them deformed (pseudoparaphyses).
b. *C. carecomoeis* var. *Litseae*. Basidiole.
c. *C. carecomoeis* var. *Litseae*. Cheilocystidia.
d. *C. excentrica*. The hymenium on the sides of the lamellae ; basidia and basidiole.

e. *C. Siparunae*. Basidia.
f. *C. minutula*. Eight pleurocystidia.
g. *C. minutula*. Five cheilocystidia.

Fig. 3. Showing spores of some species of *Crinipellis* and *Chaetocalathus*, × 900.
a. *C. sepiaria*.
b. *C. Dipterocarpi*.
c. *C. zonata*.
d. *C. campanella*.
e. *C. mirabilis*.
f. *C. carecomoeis* var. *Litseae*.
g. *C. hirticeps*.
h. *Chaetocalathus carneliorruber*.
i. *Ch. pachytrichus*.

Fig. 4. Showing some characters of *Chaetocalathus pachytrichus* and *Ch. carneliorruber*.
a. Carpophore of *Ch. pachytrichus*, × 2.
b. Hair of the pileus of *Ch. pachytrichus*, × 450.
c. Basidium of *Ch. pachytrichus*, × 450.
d. Cystidia of *Ch. pachytrichus*, the simple cystidium drawn from a specimen collected on the Philippine Islands, the forked cystidium from the same source, × 450.
e. Cystidia of *Ch. pachytrichus*, specimen collected in Tonkin, × 450.
f. Carpophore of *Ch. carneliorruber*, × 2.
g. Outline of a cystidium of *Ch. carneliorruber*, × 450.
h. Optical section of a cystidium of *Ch. carneliorruber*, × 450.
i. Hairs from the pileus of *Ch. carneliorruber*, × 450.

Plate XXIX

Armillariella ditopa Sing. Normal basidiocarpous fruiting bodies and arthrospore-bearing carpophores, the former with pileus, and clitocyboid in habit, the latter clavarioid in habit. Natural size. Photograph by R. Singer & A. P. L. Digilio.

INDEX TO THE TERMS [161]

[161] For terms of a more elementary nature whose knowledge is presumed as essential for the understanding of the present book, the author refers to starred items of « Bibliography ».

INDEX TO THE GENERA

INDEX TO THE SPECIES

TABLE OF CONTENTS

CORRIGENDA

p. 10, line 32 : historial, read : historical.
: genius inspiration, read : genius and inspiration.
p. 49, line 11 : 1, read : 2.
p. 51, line 27 : *Anthracophyllus*, read : *Anthracophyllum*.
p. 75, line 4 : XIII, read : XIV.
p. 94, line 1 : XIV, read : XV.
p. 94, line 20 : XV, read : XVI.
p. 107, line 10 : XVI, read XVII.
p. 167, line 12 : *Clytocibe*, read : *Clitocybe*.
p. 187, line 12 : C. subhirta (Peck) Peck, add : sensu Singer 1943, non Peck nec Sing. & Smith.
p. 204, line 3 from below : *N. elasticus* Sing., delete !
p. 224, line 7 : *T. prophyrophyllum*, read : *T. porphyrophyllum*.
p. 242, line 5 : *L. nauseocodulcis*, read : *L. nauseosodulcis*.
p. 270, line 15 : *Lentodiopis*, read : *Lentodiopsis*.
p. 313, line 4 : *Cyphelia cruciformis*, read : *Cyphella cruciformis*.
p. 342, last line of the key : *C. asperiformis*, read : *C. asperifolius*.
p. 370, line 17 : *Collybia aurantella*, read : *Collybia aurantiella*.
p. 381, after last line of synonymy of genus *Amanita*, add : *Amanitina* Gilb. *l. c.*
p. 421, line 2 : *Clorophyllum*, read : *Chlorophyllum*.
p. 422, line 15 : *L. inanthinofuscus*, read : *L. ianthinofuscus*.
p. 425, line 20 : *Pseudocoprinus*, read : *Leucocoprinus*.
p. 455, line 25 : *Pseudocoprinus*, read : *Xerocoprinus*.
p. 458, line 18 : *C. microrhizus*, read : *C. macrorhizus*.
p. 476, line 5 : after « clampless » add : « and several species of *Bolbitius* normally without clamp connections ».
p. 484, line 28 : hair-lide, read : Hair-like.
p. 485, line 3 : substitute « ; » by « (».
p. 485, line 12 : Metwod, read : Metrod.
p. 485, line 17 : sections 3 and 4, read : sections 1 and 2.
p. 493, line 32 (letter F), hecoming, read : becoming.
p. 518, line 20 was omitted. It should read : *Type Species : K. mutabilis* (Schaeff. ex Fr.) Sing. & Sm.
p. 569, line 12 : fora, read : forms.
p. 622, line 7 : *R. disthales*, read : *R. dysthales*.
p. 641, line 6 from below. *Phyllophorus*, read : *Phylloporus*.
p. 643, line 23 (letter B : *Phaeocyroporus*, read : *Phaeogyroporus*.
p. 657, line 7 : *S. fiavus*, read : *S. flavus*.
p. 716, line 22 : *R. citrinchlora*, read : *citrinochlora*.
p. 722, line 22 : *L. rubroviolacens*, read : *L. rubroviolascens*.